

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 44, No. 9, pp. 157-224, 33 figs., 7 tables.

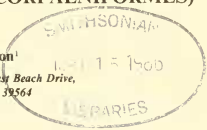
May 6, 1986

SYSTEMATIC RELATIONSHIPS AND ONTOGENY OF THE
SCULPINS *ARTEDIUS*, *CLINOCOTTUS*, AND
OLIGOCOTTUS (COTTIDAE: SCORPAENIFORMES)

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ABSTRACT: Using the methods of phylogenetic analysis proposed by Hennig (1966), characters of the larvae of 13 species of *Artedius*, *Clinocottus*, *Oligocottus* are examined in terms of synapomorphic states. Number and pattern of preopercular spines, gut diverticula, body shape, and a bubble of skin at the nape are identified as synapomorphic characters useful in systematic analysis of this group.

The synapomorphic character, multiple preopercular spines, provides strong evidence that *Clinocottus acuticeps*, *C. analis*, *C. embryum*, *C. globiceps*, *C. recalvus*, *Oligocottus maculosus*, *O. snyderi*, *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3* form a monophyletic group within the Cottidae. Within this group, the species of *Clinocottus* and *Oligocottus* are very closely related; each genus, however, appears to be monophyletic. Larvae of all species of *Clinocottus* possess the synapomorphy, auxiliary preopercular spines. Larval *Oligocottus maculosus* and *O. snyderi* share two derived characters, dorsal gut bumps and a bubble of skin at the nape. *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3* also form a monophyletic group closely related to *Clinocottus* and *Oligocottus* on the basis of a unique multiple preopercular spine pattern.

Synapomorphic characters of the larvae provide strong evidence that *A. creaseri* and *A. meanyi* are more closely related to *Icelinus* than to species of *Clinocottus*, *Oligocottus maculosus*, *O. snyderi*, *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3*. Characters of the larvae strongly indicate that the genus *Artedius* as defined by Bolin (1934, 1947) is not monophyletic and that *A. creaseri* and *A. meanyi* should be placed separately from the other species of *Artedius*. Clarification of the exact position of these two species in relation to the *Artedius-Clinocottus-Oligocottus* group and other cottids must await reexamination of characters of adults.

Complete, identified, developmental series of larval cottids *Artedius fenestralis*, *A. creaseri*, *A. meanyi*, *Oligocottus snyderi*, *Clinocottus embryum*, and *C. globiceps* are described for the first time. Partial developmental series of two species, *Artedius Type 3* and *Clinocottus analis*, are also described and illustrated for the first time. In addition, four species, *Artedius harringtoni*, *A. lateralis*, *Oligocottus maculosus*, and *Clinocottus acuticeps* are redescribed providing new and comparative information on larval development.

INTRODUCTION

The Cottidae are a large, morphologically diverse family of fishes composed of nearly 67 gen-

era and 300 species (Nelson 1976). Most of these species are marine and generally distributed in coastal waters of all oceans except the Indian Ocean. Cottids are most speciose in the North Pacific where 90 species distributed in 40 genera are reported to occur between Baja, California and the Aleutian Islands, Alaska. Sixteen of these species belonging to the genera *Artedius*, *Cli-*

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cottus, and *Oligocottus* are common intertidal and subtidal inhabitants of the northeast Pacific coast (Table 1). Despite their abundance the systematic status and early life history of members of *Artedius*, *Clinocottus*, and *Oligocottus* have received little study.

The few systematic studies that have addressed these genera have yielded contradictory results. Most workers have placed members of *Artedius*, *Clinocottus*, and *Oligocottus* in the family Cottidae (Jordan and Evermann 1898; Regan 1913; Bolin 1934, 1944, 1947; Berg 1940; Taranets 1941; Howe and Richardson 1978; Jordan (1923), however, placed the genus *Artedius* in the family Icelidae. Bolin (1934, 1947), in a review of marine cottids of California, proposed that *Artedius*, *Clinocottus*, and *Oligocottus* were closely related genera that evolved from an evolutionary line of cottids tending towards a reduction of gills, pelvic fin rays, preopercular spines, and squamation. In contrast, Taranets (1941) separated members of these genera into two subfamilies. He placed *Clinocottus*, *Oligocottus*, and five species of *Artedius* in the subfamily Oligocottinae, and placed *Artedius creaseri* and *A. meanyi* in the Icelinae. Howe and Richardson (1978) suggested that *Artedius*, *Clinocottus*, and *Oligocottus* form a closely related group, *Oligocottus* and *Clinocottus* being most closely related. However, they did not discuss characters that led to their proposal.

Much of the confusion in the systematic treatment of these genera is due to the use of primitive and reductive characters in classifications, and the failure of past workers to define the genera on the basis of unique, derived characters. Characters used in past studies have not been exclusive to this group and are present in other cottid genera.

The usefulness of characters of larvae and juveniles in elucidating systematic relationships has been demonstrated in several groups (Bertelsen 1951; Moser and Ahlstrom 1970, 1972, 1974; Johnson 1974; Okiyama 1974; Kendall 1979; Richardson 1981; and Moser et al. 1984). Results of these studies have indicated that ontogenetic characters provide an independent set of characters with which to evaluate phylogenetic relationships. Characters of larvae have been particularly helpful in groups in which characters of adults have been reductive or generalized (Moser and Ahlstrom 1972, 1974).

Although larvae of most species of *Artedius*,

Clinocottus, and *Oligocottus* are frequently collected in nearshore plankton samples in the northeast Pacific, until recently larvae of few species have been described. Of the 16 nominal species, developmental series of identified larvae have only been described for *A. harringtoni*, *A. lateralis*, *C. acuticeps*, *C. recalvus*, and *O. maculosus*. Other forms that belong to this group based on larval morphology, but not identified to species, were described by Richardson and Washington (1980) as *Artedius* Type 2, Cottidae Type 1, Type 2, and Type 3. Previous descriptions of *A. lateralis* and *O. maculosus* are inadequate for specific identification. Descriptions by Richardson and Washington (1980) were based on incomplete developmental series and too few specimens for specific and/or generic identification.

The objectives of this study were: 1) to evaluate phylogenetic relationships of *Artedius*, *Clinocottus*, and *Oligocottus* within the Cottidae following the phylogenetic methodology of Hennig (1966) and 2) to describe the ontogeny of larvae and juveniles of as many species of *Artedius*, *Clinocottus*, and *Oligocottus* as possible.

METHODS AND MATERIALS

Systematic Procedures

The investigation of systematic relationships in this study follows the phylogenetic approach first put forth by Hennig (1966) and modified and debated by Brundin (1966, 1968), Cracraft (1974), Sneath and Sokal (1973), Ashlock (1974), Mayr (1974), and others.

This methodology is considered best suited to the objectives of this study because the methodology is a phylogenetic approach, and is well defined in regard to character evolution. Other approaches currently used are not as well suited to the purpose of this study. Numerical taxonomy, best described by Sneath and Sokal (1973), is a phenetic approach in which taxa are clustered by overall similarity. Evolutionary systematics described by Mayr (1969) and Simpson (1961) combines both phyletic and phenetic information; however, a well-defined, repeatable methodology has not been incorporated into this approach.

The basic tenet of Hennig's approach is that the shared possession of derived character states is the only valid criterion for establishing phylogenetic relationships. Hennig (1966) defines a

TABLE 1. SPECIES OF *ARCTIDIUS*, *CLINOCOTTUS*, AND *OLIGOCOTTUS* AND THEIR MERISTICS.¹ (Mode is indicated in parentheses.)

	Dorsal fin spines	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Principal caudal rays	Total vertebrae ²	Branchio-stegal rays
<i>Arctidius corallinus</i>	VIII-IX (IX)	15-16 (16)	12-13 (13)	14-16 (16)	3	6 + 6	31-33 (32, 33)	6
<i>Arctidius creaseri</i>	IX-X (X)	12-14 (13)	9-11 (10)	15-17 (16)	3	6 + 6	30-31 (31)	6
<i>Arctidius fenestralis</i>	VIII-IX (IX)	16-18 (17)	12-14 (12, 13)	14-16 (15)	3	6 + 6	32-35 (35)	6
<i>Arctidius harringtoni</i>	VIII-X (IX)	15-18 (17)	10-14 (13)	13-15 (14)	3	6 + 6	32-34 (33, 34)	7
<i>Arctidius lateralis</i>	VIII-X (IX)	15-17 (16)	12-14 (13)	14-16 (15)	3	6 + 6	32-34 (33)	6
<i>Arctidius meanyi</i>	IX-X (X)	14-17 (16)	10-12 (12)	14-16 (15)	2-3 (2)	6 + 6	33-35 (34)	6
<i>Arctidius notospilotus</i>	IX-X (IX)	14-16 (15)	11-13 (12)	14-17 (16)	3	6 + 6	32-34 (32)	6
<i>Clinocottus acuticeps</i>	VIII-IX (VIII)	13-17 (15, 16)	9-13 (12)	13-15 (14)	3	6 + 6	31-33 (32, 33)	6
<i>Clinocottus analis</i>	IX-X (IX)	14-18 (16, 17)	11-14 (12, 14)	14-15 (15)	3	6 + 6	31-35 (32)	6
<i>Clinocottus embryum</i>	VIII-X (IX)	14-17 (15)	9-12 (10)	12-15 (14)	3	6 + 6	33-35 (33, 34)	6
<i>Clinocottus globiceps</i>	VIII-X (IX)	13-17 (16)	11-12 (11)	13-15 (14)	3	6 + 6	32-33 (33)	6
<i>Clinocottus recubus</i>	VIII-IX (IX)	14-16 (16)	9-13 (12)	13-15 (14)	3	6 + 6	33-34 (33)	6
<i>Oligocottus maculatus</i>	VIII-IX (VIII)	15-18 (17)	12-14 (13)	12-15 (14)	3	6 + 6	34-37 (36)	6
<i>Oligocottus rimensis</i>	VIII-X (IX)	16-19 (18)	13-15 (14)	13-15 (14)	3	6 + 6	32-35 (33)	6
<i>Oligocottus rubello</i>	VIII-IX (VIII)	15-17 (16)	12-14 (13)	13-15 (14)	3	6 + 6	34-37 (34, 35)	6
<i>Oligocottus snyderi</i>	VIII-IX (VIII)	17-20 (19)	12-15 (14)	12-15 (14)	3	6 + 6		

¹ From original counts and from compilation of Howe and Richardson (1978).² Includes hypural.³ *Arctidius* Type 3 larvae are either *A. corallinus* or *A. notospilotus*; see text for explanation.⁴ Larvae described by Morris (1951).

* Species for which larvae are described in this study.

monophyletic group as a group in which all members are descended from a single stem. The common possession of one or more derived characters is the only conclusive evidence that a group is monophyletic. Shared, plesiomorphic characters are not used because primitive character states inherited from an ancestral taxon may remain unchanged in various divergent lineages and may not be evidence of close relationship. Monophyletic groups that arose from a common stem by the same splitting process are called sister groups. Every monophyletic group, together with its sister group, constitutes a monophyletic group of higher taxonomic rank.

Since only derived character states are used in determining phylogenetic relationships, the polarity of character states was determined through outgroup comparisons. The outgroup taxa examined in this study included larvae of seven different cottid genera: *Scorpaenichthys marmoratus*, *Hemilepidotus spinosus*, *Leptocottus armatus*, *Enophrys bison*, *Myoxocephalus* sp., *Icelinus* sp., and *Radulinus asprellus*. Members of these genera are quite varied and represent several divergent lineages within the Cottidae (Bolin 1934, 1947; Taranets 1941; Howe and Richardson 1978). Larvae of several other scorpaeniform families also were examined for outgroup comparisons. These taxa included: *Sebastes flavidus* (Scorpaenidae); *Hexagrammos* sp. (Hexagrammidae), Cyclopteridae Type 1 (Cyclopteridae), and *Stellerina xyosterna* (Agonidae).

SELECTION OF CHARACTERS FOR ANALYSES.—A variety of characters were examined in *Arteidius*, *Clinocottus*, and *Oligocottus* larvae including meristics, morphology, pigmentation, spination, and developmental osteology. However, of the 50 characters initially examined, many were deleted from final analysis. The criteria used in deleting characters are as follows:

- (1) Characters that exhibit a large amount of variability were deleted from analysis. Highly variable characters are poor indicators of phylogenetic relationships (Bolin 1947; Simpson 1961; Mayr 1969). Examples of variable characters are head pigmentation and number of posttemporal-supracleithral spines.
- (2) Derived character states found in only one species were deleted. Again characters of this nature are of no value in determining intra-

group relationships. Hindgut diverticula of *Clinocottus acuticeps* are an example of a specific character.

- (3) Characters in which the sequence of change or the primitive and derived states could not be identified were deleted from the analysis. Many of the morphometric and pigmentation characters fell into this category.

Taxonomic Procedures

Larval descriptions are based on both laboratory-reared larvae and field-collected specimens. Egg masses were spawned from ripe *Clinocottus globiceps*, *Oligocottus maculosus*, and *O. snyderi* collected from tidepools along the central Oregon coast during winter-spring 1979 and 1980. Larvae were maintained at 12–13°C. In addition to reared specimens, developmental series were put together with larvae obtained with 70 cm bongo nets and neuston nets off the coast of Oregon between 1969 and 1978. Samples were taken in all months of the year from an area concentrated along an east-west transect off Newport, Oregon (lat. 44°39.1'N). Specimens were also obtained from estuarine and coastal collections of the Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service; Scripps Institution of Oceanography; Los Angeles County Museum of Natural History; Marine Ecological Consultants; California Academy of Sciences; Humboldt State University; Northwest Fisheries Center, Seattle Laboratory, National Marine Fisheries Service; and University of Washington. Reared specimens of *Arteidius lateralis* from College of Fisheries, University of British Columbia and *Oligocottus maculosus* and *Clinocottus acuticeps* from Vancouver Public Aquarium were also utilized. Transforming and juvenile specimens were collected monthly from 1977 to 1980 from tidepools along the central Oregon coast.

All specimens were preserved in 5 or 10% buffered formalin and some material was subsequently transferred to 36 or 40% isopropyl alcohol.

Developmental series of larvae and juveniles were assembled for 12 of the 16 species of *Arteidius*, *Clinocottus*, and *Oligocottus*. The number of specimens examined in each series varies from 11–38 according to availability of material. Developmental series were formed utilizing field-caught larvae, except as noted below, because of

the large amounts of variation in morphology and pigmentation in laboratory-reared larvae. Newly hatched, reared larvae are included in series of *Artedius fenestralis*, *A. lateralis*, *Clinocottus acuticeps*, *C. globiceps*, *Oligocottus maculosus*, and *O. snyderi*. In addition, reared larvae were used to supplement incomplete developmental series of field-caught larvae of *Clinocottus globiceps* and *Oligocottus maculosus*. Marked differences between developmental series based on field specimens and laboratory-reared specimens are noted in the descriptions.

Developmental stages follow the terminology of Ahlstrom et al. (1976), except that the transitional period between the larval and juvenile stages is marked by an increase in pigmentation particularly over the head and in saddles along the dorsum, a reduction in the size and number of preopercular spines, an ossification of the pelvic fin spine and rays, and the formation of scales. Specimens are referred to as juveniles when they settle from the plankton and assume a benthic existence.

MORPHOMETRICS.—Measurements of selected body parts were made to the nearest 0.1 or 0.01 mm using an ocular micrometer in a stereomicroscope. Measurements were made following the definitions of Richardson and Laroche (1979) except as follows: body depth at anus = vertical distance from the dorsal to ventral body margin at the anus, snout to pelvic fin origin = horizontal distance from the tip of the snout to a vertical through the origin of the pelvic fin, and origin of pelvic fin to anus = horizontal distance from a vertical through the origin of the pelvic fin to the anus. Head length is abbreviated as HL. Detailed tables documenting the development of meristic elements for larvae of *Artedius*, *Clinocottus*, and *Oligocottus* are presented by Washington (1981).

All body lengths given in this study refer to either notochord length (NL), which is defined as snout tip to notochord tip preceding development of the caudal fin; standard length (SL), which is defined as snout tip to the posterior margin of the hypural plates; or total length (TL), which is defined as snout tip to the posteriormost margin of the caudal fin. Unless otherwise indicated, all lengths given are standard length.

MERISTICS.—Following the methods of Dingerkus and Uhler (1977), several larvae were cleared and stained with Alcian Blue and Alizarin Red S for each species when specimens were available in sufficient numbers. Counts were

made of dorsal fin spines and rays, anal fin rays, pelvic fin spines and rays, principal caudal rays, branchiostegal rays, preopercular spines, and vertebrae. Vertebral counts always included the urostyle. All meristic elements were counted if they absorbed Alizarin stain. Principal caudal rays are defined as the number of caudal fin rays that articulate with the upper and lower hypural plates.

Counts of meristic elements were also made on unstained larvae from the developmental series used in the morphometric examination. All fin rays and spines, branchiostegal rays, preopercular spines, and myomeres were counted when visible under magnification. In this study, all fin rays and spines were counted, regardless of whether they arose from the same pterygiophore. (For detailed meristic and spination tables of developmental series of known *Artedius*, *Clinocottus*, and *Oligocottus* larvae see Washington 1981).

SPINATION.—Spine terminology generally follows Richardson and Washington (1980) in which spines are named for the bones from which they originate.

TAXONOMIC TERMINOLOGY.—Results of this study do not agree with previously recognized limits of the genus *Artedius*. In order to avoid confusion, species in this group are designated as *Artedius* Group A including *A. fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3* (either *A. corallinus* or *A. notospilotus*) or *Artedius* Group B including *A. creaseri* and *A. meanyi*. Larvae referred to as *Artedius* Type 3 are either *A. corallinus* or *A. notospilotus*. Positive identification is not possible at this time because of the lack of late-stage larval specimens. (See descriptions for discussion of identification.)

RESULTS

Description of Characters Considered

PREOPERCULAR SPINATION.—The number of preopercular spines is a relatively stable, conservative character in larval cottids. Most cottid larvae (22 of 28 known genera) possess four approximately equal-sized spines situated along the posterior margin of the preopercle. Generally the dorsalmost spine increases in size with development while the lower three spines are reduced or lost.

A modification of this basic preopercular pattern is found in larvae of several species of *Ice-*

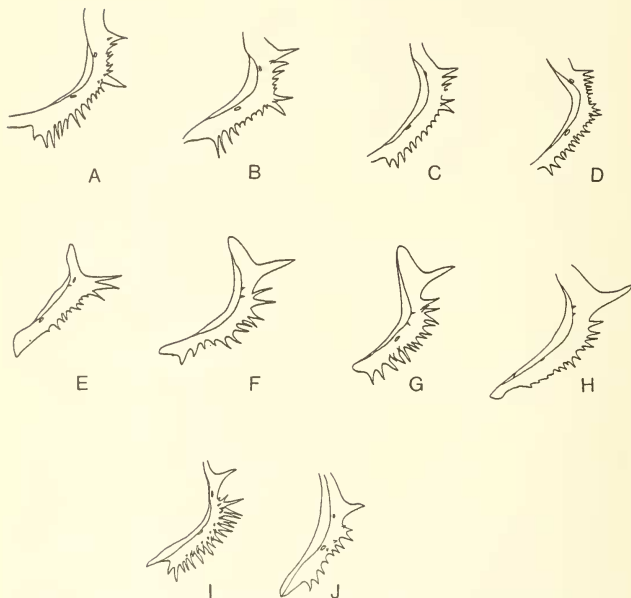


FIGURE 1. Multiple preopercular spines in larval *Artedius*, *Clinocottus*, and *Oligocottus*. A) *Artedius harringtoni*, B) *A. fenestralis*, C) *A. lateralis*, D) *A. Type 3*, E) *Clinocottus acuticeps*, F) *C. embryum*, G) *C. globiceps*, H) *C. analis*, I) *Oligocottus snyderi*, J) *O. maculosus*.

linus and *Myoxocephalus*. These larvae possess an additional small, auxiliary spine situated on the inner shelf of the preopercle anterior to the bases of the four principal preopercular spines.

A third pattern of preopercular spination is found in larvae of *Clinocottus*, *Oligocottus*, and *Artedius* Group A (Fig. 1). These larvae possess 5–24 small spines situated along the posterior margin of the preopercle. Two basic patterns of multiple preopercular spines occur in larvae of this group. In four species of *Artedius* (Group A), the dorsalmost, middle, and ventralmost spines become enlarged relative to the other preopercular spines. During transformation, the dorsal-

most spine continues to increase in size, while the middle spines (7–9), midventral spines (11–14), and ventralmost spines each fuse together, forming three large bumps on the preopercular margin. The other preopercular spines gradually disappear.

In larvae of *Clinocottus* and *Oligocottus* the dorsalmost spine increases in size relative to the other preopercular spines. During transformation the lower spines regress and disappear while the dorsalmost spine remains prominent.

Outgroup comparisons with larvae of closely related Scorpaeniformes indicate the presence of five or fewer approximately equal-sized pre-



FIGURE 2. Preopercular spines of larval *Arctedius meanyi* and *A. creaseri*.

opercular spines. *Sebastes* and *Stellerina* larvae possess five and four spines, respectively; hexagrammid larvae possess five to six, three, or no spines, and cyclopterid larvae have lost all preopercular spines. The cottid taxa that possess four equal-sized preopercular spines also tend to have many other primitive character states. The presence of four equal-sized spines is considered the plesiomorphic state for preopercular spines in cottid larvae.

The modified pattern of spines found in larval *Icelinus* and *Myoxocephalus* could easily be derived from the basic pattern of four preopercular spines. In fact, larvae of several species of *Icelinus* and *Myoxocephalus* possess only four preopercular spines. The presence of an auxiliary spine on the preopercle probably represents an intermediate character state leading toward multiple preopercular spines.

The multiple preopercular spines of larvae of *Arctedius* (Group A), *Clinocottus*, and *Oligocottus* are unique to this group. Multiple preopercular spines are not present in any other known cottid or scorpaeniform larvae. Multiple preopercular spines are derived character states indicative of the monophyletic origin of this group.

BASAL PREOPERCULAR SPINE.—Larvae of *Arctedius meanyi* and *creaseri*, larvae of at least two species of *Icelinus*, and larvae of *Myoxocephalus* possess small projections or spines on the base of each of the four main preopercular spines (Fig. 2). These basal spines project out at 90° angles to the axis of the main preopercular spines. The basal spines are most pronounced in early postflexion larvae. With development, four bony

ridges form on the inner shelf of the preopercle, parallel to each basal spine. These bony ridges grow toward the basal spines and gradually fuse with them, forming bony arches over the forming lateral line canal of the preopercle. These basal spines are not present in other cottid or scorpaeniform larvae examined and probably are a derived character state.

INNER SHELF PREOPERCULAR SPINES.—Larval *Clinocottus* possess one or two tiny spines on the inner shelf margin of the preopercle. *Clinocottus acuticeps* larvae have only one inner shelf spine. All other *Clinocottus* larvae examined have two. These spines are transient features which form in postflexion larvae and are lost before transformation. They appear to be unique to this group and, as such, to be derived character states.

NAPE BUBBLE.—Larvae of *Oligocottus maculosus* and *O. snyderi* possess a distinctive bubble of skin in the nape region just anterior to the origin of the dorsal fin (Fig. 3). This bubble is present at hatching and persists for two or three weeks (to about the beginning of flexion of the notochord). No other known cottid larvae possess a bubble of skin at the nape; accordingly, this bubble is probably a derived character unique to these two species. (Larvae of *O. rimensis* and *O. rubellio* are unidentified and it is not known if they also possess this character.)

GUT DIVERTICULA.—Long protrusions or diverticula extend dorsolaterally from either side of the abdominal cavity in larvae of *Arctedius fenestralis*, *A. lateralis*, and *A. Type 3* (Fig. 4). These diverticula are present at hatching and persist throughout larval development. Newly

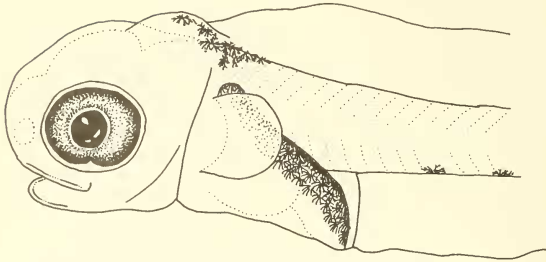


FIGURE 3. Nape bubble of larval *Oligocottus snyderi*.

hatched larvae of *Oligocottus maculosus* and *O. snyderi* possess similar but less pronounced bumps or protrusions on either side of the dorsal surface of the abdominal cavity. These bumps are present at hatching, but they disappear after two to three weeks at about the onset of notochord flexion. The diverticula of *Artedius fenestralis*, *lateralis*, and Type 3 and the smaller protrusions of *Oligocottus* appear to be homologous structures, with the smaller bumps constituting an intermediate form. These diverticula are unique, derived characters not known in other cottid larvae.

Larvae of *C. acuticeps* also possess long diverticula which extend posteriorly on either side of the anus. Larvae of *C. globiceps*, *C. embryum*, and *C. analis* have bulges on either side of the anus. Although these bulges appear to form an intermediate state in the evolution of hindgut diverticula, histological sections of the guts of larval *Clinocottus* yielded inconclusive results. Larval *C. analis*, *C. embryum*, and *C. globiceps* possess an enlarged coelom on either side of the hindgut, but no distinct diverticula. Hindgut diverticula appear to be unique to *C. acuticeps*.

PARIETAL AND NUCHAL SPINES.—Most larval cottids develop two spines, a large anterior parietal and a smaller posterior nuchal spine at the posterior edge of the parietal bones. The anterior parietal spine develops first, followed by a smaller nuchal spine that forms just posterior to it. These spines are generally transient structures that form late in larval development and are reduced or lost during transformation. In many

species of cottids, the spines appear to fuse together enclosing a small canal between the bases of the two spines. This canal eventually becomes part of the cranial lateral line system. In other species, the spines decrease in size without fusing together. Concurrently, sheets of bone extend anteriorly and posteriorly from the spines and eventually fuse together, forming an incipient cranial arch.

Similar parietal and nuchal spines occur in larvae of most other scorpaeniform families and appear to be homologous to those of cottid larvae. The presence of a parietal and nuchal spine is probably the primitive or ancestral condition in the Cottidae.

Parietal and nuchal spines have undergone modification and elaboration in larvae of most of the species of *Clinocottus* and *Oligocottus*, and in *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3*. Two species (*Artedius harringtoni* and *Clinocottus acuticeps*) have lost these spines completely. Three species (*Clinocottus analis*, *C. embryum*, and *C. recalvus*) have retained the primitive condition of possessing a parietal and nuchal spine. The remaining species (*A. fenestralis*, *A. lateralis*, *O. maculosus*, *O. snyderi*, and *C. globiceps*) have tended toward an elaboration and increase in number of parietal spines. Generally, these larvae develop a cluster of three to six spines, which are situated in two transverse rows at the posterior margin of the parietal region. During transformation, these clusters of spines decrease in size and disappear. At the same time, sheets of bone extend ante-

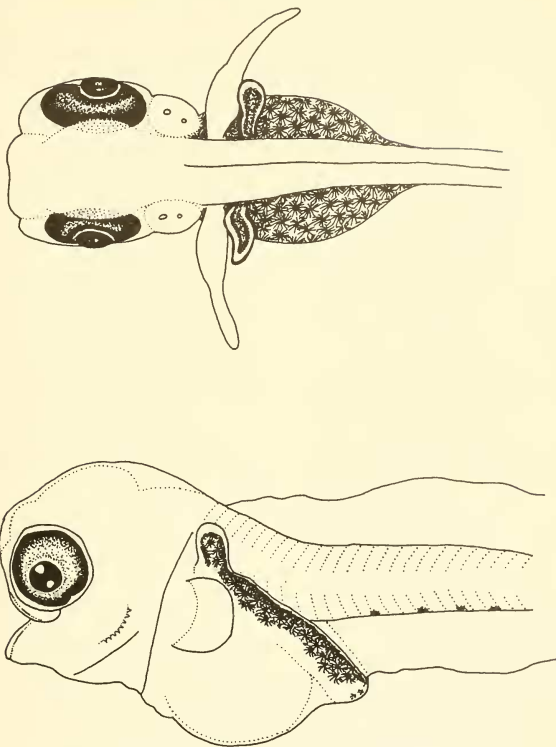


FIGURE 4. Dorsal gut diverticula in larval *Artedius fenestralis*.

riorly and posteriorly from the bases of the two rows of spines and eventually fuse together. This bony arch becomes a part of the cranial lateral line system in juveniles.

The absence of parietal spines in *A. harringtoni* and *C. acuticeps* is probably a secondary loss and, as such, represents a derived condition. The

elaboration of spines into clusters is apparently unique to larvae of *Artedius*, *Clinocottus*, and *Oligocottus* and is also a derived state.

PIGMENTATION.—Melanistic pigmentation varies greatly among cottid larvae ranging from relatively unpigmented forms to heavily pigmented ones. Larvae of *Artedius*, *Clinocottus*, and

Oligocottus are all lightly pigmented and possess numerous, intense melanophores over the dorsolateral surface of the gut and in a row posterior to the anus. The shape and number of midline melanophores varies between species. Larvae of all but one species, *A. creaseri*, possess several melanophores in the nape region. The presence of head pigment and anteroventral gut melanophores varies among the species of *Arteidius*, *Clinocottus*, and *Oligocottus*.

Although pigment patterns are diagnostic at the specific level, they are difficult to evaluate for use in systematic analysis. Many fish larvae in distantly related families, and even orders, are similarly pigmented. Several cottid genera other than *Arteidius*, *Clinocottus*, and *Oligocottus* also possess similar pigment patterns. Hence, it is difficult, if not impossible, to determine which pigment patterns are primitive and which are derived.

Nevertheless, trends in certain areas of pigmentation can be discerned. Among known cottid larvae, a discrete nape pigment patch is found only in members of *Arteidius*, *Clinocottus*, *Oligocottus*, *Enophrys*, *Myoxocephalus*, and *Gymnocanthus*. Nape pigment is probably derived in cottid larvae. The number of ventral midline melanophores situated posterior to the anus ranges from 2 to 33 in larvae of *Arteidius*, *Clinocottus*, and *Oligocottus*. In addition, the shape and spacing of these melanophores varies from small dots to long slashes extending onto the ventral finfold to large pigment blotches. *Arteidius creaseri* and *A. meanyi* both possess irregularly shaped blotches of pigment along the ventral midline. *Arteidius fenestralis*, *A. harringtoni*, and *A. lateralis* all possess distinctive pigment slashes. *Oligocottus* and *Clinocottus* larvae possess small, round melanophores. Although these pigment patterns bind certain species together, it is difficult to determine ancestral versus derived states. Both pigment blotches and distinctive midline slashes are found in larval *Icelinus*. Pigment, as well as other characters, indicates that *Icelinus* shares close affinities with *Arteidius*; however, the direction of the evolution of pigment patterns cannot be determined.

MORPHOMETRICS.—Cottid larvae exhibit a diversity of body forms. Body shape ranges from short and stubby (*Arteidius* [Group A] and *Enophrys*) to long and slender (*Radulinus* and *Icelus*) to globose (*Malacocottus*). Larval *Arteidius* (Group

A), *Clinocottus*, and *Oligocottus* have short, stubby bodies with blunt, rounded snouts. Gut length is moderately long and the posterior portion of the hindgut trails well below the rest of the body.

Measurements of body parts frequently overlap in larval *Arteidius* (Group A), *Clinocottus*, and *Oligocottus* because of their similarity in body shape. These similarities make it difficult to determine discrete character states or transformation series. In addition, many body parts change markedly during larval development, frequently exhibiting allometry. Because of the extreme diversity of forms found in larval cottids, it is difficult to evaluate morphometric characters for systematic analysis. Trends can be observed in only a few body parts.

Larvae of *Arteidius creaseri* and *A. meanyi* have long, pointed snouts. They develop relatively long ascending processes on the premaxillary. The underlying ethmoid cartilage is relatively large, causing a pointed, humped appearance of the snout. Larval *Icelinus* exhibit pointed snouts similar to that of *A. meanyi* and *A. creaseri*.

In contrast, all other larval *Arteidius*, *Clinocottus*, and *Oligocottus* have blunt, rounded snouts. The ascending processes of their premaxillaries are relatively short, and the ethmoid cartilage forms late in development.

Snout length is variable in the outgroup taxa. *Sebastes* larvae have a somewhat long, pointed snout, but the hexagrammid, cyclopterid, and agonid larvae examined have shorter, rounded snouts. Within the cottids, *Enophrys*, *Leptocottus*, *Hemilepidotus*, and *Scorpaenichthys* larvae all have blunt, rounded snouts. This condition is probably the primitive condition relative to larvae of *Arteidius*, *Clinocottus*, and *Oligocottus* because it is widespread in several divergent genera of cottids and scorpaeniforms. The pointed snout appears to be a derived condition.

Although gut length varies greatly among cottid larvae (Richardson and Washington 1980), larval *Arteidius* (Group A), *Clinocottus*, and *Oligocottus* possess distinctive guts with the hindgut coiled very loosely and extending posteriorly. The tip of the hindgut extends ventrally well below the rest of the body and posteriorly to the origin of the anal fin. This condition is most pronounced in *Clinocottus* larvae. Larval *C. acuticeps* and *C. embryum* have especially long, trailing hindguts which extend posteroventrally past

the anal fin origin. A trailing gut is unique to larvae of *Artedius* (excepting *A. meanyi* and *A. creaseri*), *Clinocottus*, and *Oligocottus*, and is assumed to be a derived condition.

PELVIC FIN RAYS.—The number of pelvic fin rays in cottids ranges from one spine and five rays to no spines or rays.

Pelvic fin rays are generally considered to be undergoing reduction in the cottids. The primitive state is 1,5 fin rays as in other Scorpaeniformes. Reduction in number of rays is a derived state.

Larvae of *Artedius*, *Clinocottus*, and *Oligocottus* all possess 1,3 pelvic fin rays, except for *A. meanyi*. *Artedius meanyi* usually possesses 1,2 pelvic fin rays. The outermost of these fin rays is markedly long and thickened, and the tips of this ray are separated. *Icelinus* also possesses 1,2 pelvic fin rays; however, both rays are relatively short and fine. The thickened outer ray of *A. meanyi* may have evolved through the fusion of two fin rays. If so, this condition may constitute an intermediate state between the three pelvic fin rays of *Artedius*, *Clinocottus*, and *Oligocottus* and the two pelvic fin rays of *Icelinus*.

BRANCHIOSTEGAL RAYS.—The scorpaenids, considered to be the most generalized scorpaeniform (Bolin 1947; Quast 1965), possess seven branchiostegals. The hexagrammids and the zaniolepidids, which occupy an intermediate position between the scorpaenids and cottids (Quast 1965), both possess six branchiostegals. Most cottids possess six branchiostegal rays; however, the psychrolutids and some freshwater *Cottus* species have seven branchiostegals. The psychrolutids are a distinct group which possess many derived characters and have apparently diverged from other cottids. Similarly, members of *Cottus* also possess many derived characters that apparently reflect adaptation to a freshwater habitat. Cottids that are generally considered to be primitive because they retain many primitive features all possess six branchiostegal rays.

Although the possession of seven branchiostegal rays is probably the primitive condition in the scorpaeniforms, possession of six branchiostegals appears to be the primitive state within the cottids. Cottid genera such as *Icelinus* and *Hemilepidotus*, which Bolin (1947) considered to have evolved from the evolutionary line leading to *Artedius*, *Clinocottus*, and *Oligocottus*, all possess six branchiostegal rays. Six branchioste-

gals is probably also the primitive state relative to *Artedius*, *Clinocottus*, and *Oligocottus*. Because those cottids generally considered to be from the same evolutionary lineage as *Artedius* (Bolin 1934, 1947) all have six branchiostegals, it is assumed that the seven branchiostegals found in *Artedius harringtoni* and in some *Clinocottus globiceps* are secondarily derived.

POSTTEMPORAL-SUPRACLEITHRAL SPINES.—Larvae of most known scorpaeniforms (including most known cottids) develop three spines in the posttemporal-supracleithral region of the head. Generally, two spines form first on the ventral portion of the posttemporal bone, and one spine forms midway along the posterior margin of the supracleithrum. These spines persist during transformation at which time the surrounding portions of the posttemporal and supracleithral bones undergo modification and canals form in these bones between the spines. This entire complex then develops into the junction point of the cephalic lateral line system and the lateral line system. This pattern of spines probably represents the plesiomorphic condition in larval cottids.

In larvae of *Artedius*, *Clinocottus*, and *Oligocottus* the posttemporal-supracleithral spines are frequently modified. The modifications appear to be correlated with those of the parietal and nuchal spines. Larvae that have lost parietal spines do not develop posttemporal-supracleithral spines, and larvae that have evolved complex clusters of parietal spines also develop clusters of posttemporal-supracleithral spines. Neither *A. harringtoni* nor *C. acuticeps* larvae develop any spines in the posttemporal-supracleithral region. Larvae of *A. creaseri*, *A. meanyi*, *C. embryum*, and *C. recalvus* possess two posttemporal and one supracleithral spine. *Artedius fenestralis*, *A. lateralis*, *O. maculosus*, *O. snyderi*, and *C. globiceps* all develop more than three posttemporal-supracleithral spines.

As described for parietal and nuchal spines, the posttemporal-supracleithral spines vary among species of *Artedius*, *Clinocottus*, and *Oligocottus*. This variability among closely related species suggests that these spines may be undergoing rapid modification in this group and loss of spines or possession of clusters of spines may represent convergent or parallel evolution.

As with the parietal and nuchal spines, the absence of posttemporal-supracleithral spines in

TABLE 2. CHARACTER STATES USED IN SYSTEMATIC ANALYSIS AND THEIR DISTRIBUTION AMONG LARVAL *ARTEDIUS*, *CLINOCOTTUS*, AND *OLIGOCOTTUS* AND THE OUTGROUP TAXA.

	No. of preopercular spines		Preopercular spine pattern			Basal preopercular spine		Auxiliary preopercular spines			Bubble of skin at nape	
			Equal-sized	Dorsal spine largest	Dorsal, mid, & ventral spine largest	Absent	Present	Absent	One	Two	Absent	Present
	≤5	>5										
<i>Arteidius fenestralis</i>		X			X	X		X				X
<i>Arteidius harringtoni</i>		X			X	X		X				X
<i>Arteidius lateralis</i>		X			X	X		X				X
<i>Arteidius</i> Type 3		X			X	X		X				X
<i>Oligocottus maculosus</i>		X		X		X		X				X
<i>Oligocottus snyderi</i>		X		X		X		X				X
<i>Clinocottus acuticeps</i>		X		X		X			X			X
<i>Clinocottus analis</i>		X		X		X				X		X
<i>Clinocottus embryum</i>		X		X		X				X		X
<i>Clinocottus globiceps</i>		X		X		X				X		X
<i>Clinocottus recalvus</i>		X		X		X				X		X
<i>Arteidius creaseri</i>	X		X				X	X				X
<i>Arteidius meanyi</i>	X		X				X	X				X
<i>Scorpaenichthys marmoratus</i>	X		X			X		X				X
<i>Hemilepidotus hemilepidotus</i>	X		X			X		X				X
<i>Leptocottus armatus</i>	X		X			X		X				X
<i>Enophrys bison</i>	X		X			X		X				X
<i>Myoxocephalus</i> sp.	X		X				X	X				X
<i>Icelinus</i> sp.	X		X				X	X				X
<i>Radulinus asprellus</i>	X		X					X				X
<i>Sebastes flavidus</i>	X		X					X				X
<i>Hexagrammos</i> sp.	*		*			*		X				X
Cyclopteridae												
Type 1	*		*			*		X				X
<i>Stellerina xyosterna</i>	X		X			X		X				X

* Character absent.

A. harringtoni and *C. acuticeps* is probably a secondary loss and hence a derived state. The trend toward an elaboration of these spines is found only in members of *Arteidius*, *Clinocottus*, and *Oligocottus* and is also considered a derived state.

CHARACTERS SELECTED FOR SYSTEMATIC ANALYSIS.—Of the 50 characters examined, 10 characters were selected for use in the phylogenetic analysis (Table 2). These 10 best fit the

criteria for character selection listed in the methods.

Character 1: Number of preopercular spines.

- A) 5
- B) 0
- C) 4
- D) >5

Character 2: Preopercular spine pattern.

- A) preopercular spines equal-sized

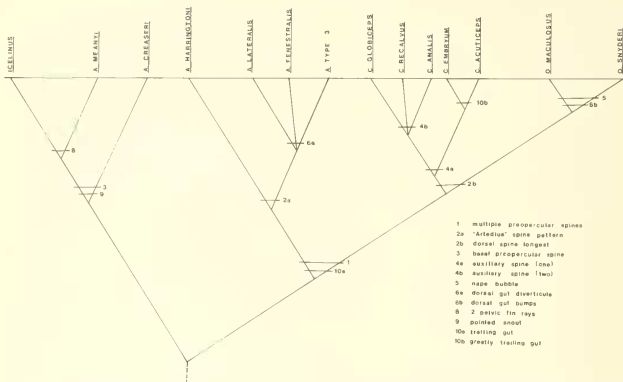


FIGURE 5. Cladogram of systematic relationships between *Artedius*, *Clinocottus*, and *Oligocottus*. Characters numbered on cladogram indicate synapomorphies.

Character 7: Parietal spines.

- A) 2
- B) modified: clusters of spines
- C) modified: absent

Character 8: Number of pelvic fin rays.

- A) >3
- B) 3
- C) 2

Character 9: Snout shape.

- A) rounded
- B) pointed

Character 10: Hindgut shape.

- A) compact; not trailing below body; ending anterior to anal fin origin
- B) hindgut trailing slightly below body; extending to origin of anal fin
- C) hindgut trailing well below body; extending posterior to anal fin origin

PHYLOGENETIC RELATIONSHIPS

A hypothesis of evolutionary relationships among species in the cottid genera *Artedius*, *Clinocottus*, and *Oligocottus* is presented in Figure 5. Two main lineages or sister groups of *Artedius*, *Clinocottus*, and *Oligocottus* larvae are repre-

sented in the resulting cladogram based on shared derived characters of the larvae. Species with larvae possessing the synapomorphic characters, multiple preopercular spines and trailing guts, form one major group. In addition to the possession of shared, derived characters, larvae of this group are extremely similar in pigmentation and body shape. The second major evolutionary line consists of species sharing two derived characters, basal preopercular spines and pointed snouts. This line includes *Artedius creaseri*, *A. meanyi*, and *Icelinus*.

The two main evolutionary lines or groups of *Artedius*, *Clinocottus*, *Oligocottus*, and *Icelinus* correspond to Taranets's (1941) classification of these species. Taranets (1941) placed *Artedius meanyi* and *A. creaseri* in the subfamily Icelinae, along with members of *Icelinus* and *Chitonotus*. He based this decision on the following characters: the upper preopercular spine larger than the lower spines; two rows of bony plates on the body—one along the lateral line, the other at the base of the dorsal fins; and scales usually present on other parts of the body. All of these characters are undergoing reduction and are present in several different genera of cottids. As such, they have

low systematic value. Taranets (1941) combined *Clinocottus*, *Oligocottus*, *Arteidius corallinus*, *A. fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. notospilotus* in the subfamily Oligocottinae. This subfamily was characterized by the absence of spines or ridges projecting through the skin on the head, weakly developed preopercular spines, body naked or with bony plates reduced, and "... other characters." Unfortunately, Taranets did not mention which other characters he examined.

In contrast, other investigators have placed *Arteidius meanyi* and *A. creaseri* in the genus *Arteidius* along with the five other species of *Arteidius* discussed above. Howe and Richardson (1978) and Bolin (1947) proposed that although *Arteidius* shared close affinities with *Icelinus*, it was more closely related to *Clinocottus* and *Oligocottus*. Jordan (1923), however, stated that *Arteidius* was most closely related to *Icelinus* because of the common possession of bony plates on either side of the dorsal fins.

The evolutionary lineage (Fig. 5) containing larvae with multiple preopercular spines includes three distinct groups of species. One of these groups includes all the species of the genus *Clinocottus*. Larvae of this group share one synapomorphic character, inner-shelf preopercular spines. Larvae of *Clinocottus* possess one or two auxiliary spines on the inner preopercular shelf. These spines appear to be a derived character unique to members of this genus and provide evidence that the genus is monophyletic. This genus has been previously recognized and defined on the basis of adult characters, e.g., loss of scales, an advanced anus, and possession of a heavy, blunt penis (Hubbs 1926; Bolin 1934, 1944, 1947; Taranets 1941; Howe and Richardson 1978). None of these characters is unique to members of *Clinocottus*. Several different lineages of cottids exhibit reduction in squamation, advanced anuses, and penes.

Within the genus *Clinocottus*, *C. embryum* and *C. acuticeps* are grouped together on the basis of a synapomorphic character, a trailing hindgut which extends posterior to the origin of the anal fin. *Clinocottus acuticeps* larvae are unique in their possession of the autapomorphy, distinct hindgut diverticula. *Clinocottus embryum* and *C. acuticeps* larvae also are similar in possessing moderately pointed snouts relative to the blunt, rounded snouts of other *Clinocottus* larvae, a

loose bubble of skin in the head region, and light pigmentation.

Synapomorphic characters for clarifying interspecific relationships among *C. analis*, *C. recalvus*, and *C. globiceps* were not identified. Nevertheless, several pigmentation and morphological characters, for which direction of evolution is not known, do suggest possible relationships among these species. Both *Clinocottus globiceps* and *C. recalvus* larvae have intense pigmentation over the snout, head, and nape. Both have very blunt, globose heads, large bulging guts, and relatively deep bodies. Juveniles of the two species are nearly inseparable based on external morphology. These characters suggest that *C. globiceps* and *C. recalvus* may be a very closely related species pair. Postflexion larvae of *C. analis* differ from all other postflexion *Clinocottus* larvae in possessing an intense band of melanistic pigment over the lateral surface of the body. Unfortunately, the polarity (direction of evolution) of many of the transformation series of morphometric and pigment characters could not be determined; hence, these characters could not be used in the phylogenetic analysis. Pigmentation and morphometric characters have been useful in several systematic studies based on larvae and have frequently been correlated with other derived characters (Johnson 1974; Moser and Ahlstrom 1974; Okiyama 1974; Richardson 1981). Clarification of relationships among the species of *Clinocottus* must await identification of derived characters or a better understanding of the evolution of pigmentation and body shape within cottid larvae.

The relationships among species of *Clinocottus* postulated by Bolin (1947) are in close agreement with relationships suggested by larval characters. Bolin placed *C. acuticeps* in its own subgenus because of its unique possession of a modified penis with a tri-lobed tip, and a membrane connecting the innermost pelvic fin ray with the abdomen. Bolin also placed *C. analis* in its own subgenus because of the retention of minute prickles covering the body. All other members of the genus are scaleless. *Clinocottus embryum*, *C. globiceps*, and *C. recalvus* were placed in the same subgenus because of their large, rounded heads and the retention of a pore behind the last gill. The latter character is plesiomorphic and, hence, of little value for evaluating relationships. Bolin (1947:163) described *C. recalvus* and *C.*

globiceps as "two extremely closely related species" because of their hemispherical head shape, an increased number of cirri on the head, and a pair of lateral knobs near the tip of the penis.

Another group of species within the lineage having multiple preopercular spines consists of *Oligocottus maculosus* and *O. snyderi*. They share two synapomorphies—a bubble of skin at the nape, and dorsal gut bumps. Larval *O. rimensis* and *O. rubellio* are not yet identified and, therefore, it is not known if these larvae also possess the synapomorphic characters binding *O. snyderi* and *O. maculosus* together.

Bolin (1934, 1947) defined the genus *Oligocottus* on the basis of the following adult characters: absence of scales; presence of a long, slender, simple penis; and modification of the anterior anal fin rays in males. Only the last character appears to be unique to members of this genus. As mentioned above, evolution of penes and loss of scales have occurred in several diverse cottid genera. Bolin placed *O. maculosus*, *O. snyderi*, and *O. rubellio* in the same subgenus because of the greatly modified anal fin in males, a permanently external penis, and loss of all but lateral line scales. He further speculated that *O. maculosus* was the least specialized member of the subgenus and *O. rubellio* was the most specialized.

Larval *O. snyderi* possess the derived, autapomorphic characters of multiple prickles covering the parietal and posttemporal regions of the head. In addition, larval *O. snyderi* possess an accessory spine at the anterior base of most of the main spines on the posterior margin of the preopercle. Both of these conditions are unique specializations of larval *O. snyderi*. Clarification of relationships of other *Oligocottus* species must await identification of larval *O. rimensis* and *O. rubellio*.

Larval characters indicate that while *Oligocottus* and *Clinocottus* are each a monophyletic group, they are closely related. Larvae of both genera are linked together into a higher-level monophyletic unit by the possession of a distinctive preopercular spine pattern.

Taranets (1941) also concluded that *Oligocottus* and *Clinocottus* are closely related. He placed both genera in the supragenus *Oligocottini* because of the presence of a penis and the absence of bony plates in both groups.

Artedius fenestralis, *A. harringtoni*, *A. lateralis*, and *A. Type 3* form the third group of larvae with multiple preopercular spines. These larvae share one synapomorphy, an *Artedius*-type preopercular spine pattern. In addition, larvae of this group possess distinctive pigment slashes on the ventral midline posterior to the anus and a strongly humped appearance in the nape region. Known larvae of *Oligocottus* and *Clinocottus* do not possess either of these characters; however, larvae of several species of *Icelinus* and *Myoxocephalus* do possess similar pigment slashes on the ventral midline. Although these characters are not unique to *Artedius* species, they provide additional support for the cohesiveness of this group.

Within the *Artedius* group, *A. fenestralis*, *A. lateralis*, and *A. Type 3* form a distinct subgroup. Larvae of these species share one synapomorphic character, dorsal gut diverticula. Characters identified in this study do not define relationships among these three species. *Artedius harringtoni* is probably less specialized than the three species possessing gut diverticula. *Artedius harringtoni* is further distinguished from other *Artedius* larvae by the possession of seven branchiostegal rays. All other cottid larvae examined in this study possess six branchiostegal rays except several laboratory-reared *Clinocottus globiceps*. Although seven rays are probably a primitive character in scorpaeniforms, *A. harringtoni* appears to have secondarily derived this condition, since none of the outgroup cottids have seven branchiostegals.

This grouping of *Artedius* larvae with multiple preopercular spines corresponds to Taranets's (1941) classification. He placed *Artedius coralinus*, *A. fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. notospilotus* together in the supragenus *Artediini* in the subfamily *Oligocottinae*.

Other workers have placed all species of *Artedius* in the same subfamily and genus (Hubbs 1926; Bolin 1934, 1947; Rosenblatt and Wilkie 1963; Howe and Richardson 1978). Bolin (1947: 161) included *A. creaseri* in *Artedius* because of the retention of hemilepidotid-like scales "in various degrees of reduction," large head, an unadvanced anus, and "normal structure of the pelvic fins."

Artedius meanyi was not reported to occur off California at the time of Bolin's work. Hence, he did not include this species in his classification.

Rosenblatt and Wilkie (1963) described *A. meanyi* as being extremely similar to *A. creaseri* and placed it in Bolin's subgenus *Ruscariops* along with *A. creaseri*.

Reduction in squamation and number of pelvic fin rays is found in many different cottid genera and appears to have evolved separately several times. *Icelinus*, *Chitonotus*, and *Orthonopias* also possess hemilepidotid-like scales in various degrees of reduction. Several species of *Icelinus*, *Orthonopias*, and *Chitonotus* possess large heads and unadvanced anuses.

Characters of the larvae indicate that *Artedius creaseri* and *A. meanyi* form a distinct grouping separate from the other species of *Artedius*. Two synapomorphic characters, a pointed snout and basal preopercular spines provide strong evidence that *A. creaseri*, *A. meanyi*, and *Icelinus* form a monophyletic group. In addition, *A. meanyi*, *A. creaseri*, and *Icelinus* larvae are very similar in other pigmentation, morphometric, and spination characters, giving further support for the cohesiveness of this group. In a phenetic study of larval cottids, Richardson (1981) also placed *A. meanyi* in a group with *Chitonotus*, *Paricelinus*, *Triglops*, and *Icelus*. (*A. meanyi* was misidentified as *Icelinus* spp. in Richardson's study. See literature section of *A. meanyi* description.) Although her study was based on similarities of the larvae and not synapomorphies, it supports the grouping of *A. meanyi* and *A. creaseri* with *Icelinus*.

Both phenetic and synapomorphic characters of the larvae provide strong evidence that the genus *Artedius* (as defined by Bolin 1934, 1947) is not monophyletic and that *A. creaseri* and *A. meanyi* should be placed separately. *Artedius meanyi* and *A. creaseri* appear to be more closely related to species of *Icelinus* and other members of Richardson's Group 2 than to other species of *Artedius*. Clarification of relationships among *A. meanyi* and *A. creaseri* must await a reexamination of characters of adult *Artedius*.

Although larvae of the *A. meanyi-creaseri* group and the *Artedius-Clinocottus-Oligocottus* group are distinct from one another, they share certain similarities in comparison to other cottid larvae. Both groups have similar pigment patterns, morphology, and meristics, suggesting that species of these two groups share a common ancestor. Bolin (1947:159) also speculated that *Icelinus*, *Chitonotus*, *Artedius*, *Clinocottus*, and

Oligocottus constitute a single evolutionary line within the Cottidae. He suggested that "certain details of the more primitive members, particularly the scales, indicate that while these forms undoubtedly did not spring from the modern genus *Hemilepidotus*, they shared a common and not particularly remote ancestor with the fishes of that genus." Although characters of the larvae do not exclude the possibility of a hemilepidotid-type ancestor, they do indicate that it would be a relatively distant ancestor. Larval *Hemilepidotus* differ markedly from larvae of *Artedius*, *Clinocottus*, *Oligocottus*, and *Icelinus* in many characters including meristics, morphometrics, osteology, spination, and pigmentation. It is much more likely that the ancestor of this group possessed characteristics similar to both the *Artedius-Icelinus* group and the *Artedius-Clinocottus-Oligocottus* group. Larvae of at least one species of *Icelinus* and several species of *Myoxocephalus* possess a fifth or sixth accessory preopercular spine. Larvae of *Myoxocephalus* also possess two distinct patterns of pigment: one type is lightly pigmented similar to the two *Artedius* groups, whereas the other has intense bands of lateral pigmentation. An ancestor similar to *Icelinus* or *Myoxocephalus* may well have given rise to *Artedius*, *Clinocottus*, *Oligocottus*, and *Icelinus*. This hypothesis is supported by the presence of one or two accessory preopercular spines in *Myoxocephalus* larvae. This preopercular spine condition appears to be intermediate between the primitive pattern of four preopercular spines and the derived pattern of multiple preopercular spines. Hence, larvae of the ancestor of *Artedius*, *Clinocottus*, and *Oligocottus* were probably relatively lightly pigmented with melanophores present on the head, nape, dorsal surface of the gut, and along the ventral midline posterior to the anus. In addition, the ancestral larvae probably possessed four large preopercular spines with one accessory spine on the inner preopercular shelf, two parietal spines, and three posttemporal-supracleithral spines.

In summary, the hypotheses of relationships between *Artedius*, *Clinocottus*, and *Oligocottus* based on larvae characters is in general agreement with previous classifications based on adult characters. Synapomorphic characters of the larvae provide strong evidence that *Clinocottus*, *Oligocottus maculosus*, *O. snyderi*, *A. fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3 form*

a monophyletic group within the cottids. Within this group, the genera *Clinocottus* and *Oligocottus* are very closely related; however, each genus appears to be monophyletic. *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3* also form a monophyletic species group closely related to *Clinocottus* and *Oligocottus*. However, synapomorphic characters of the larvae provide strong evidence that *A. creaseri* and *A. meanyi* are more closely related to *Icelinus* than to species of *Clinocottus*, *Oligocottus*, and other *Artedius*. The genus *Artedius* as defined by Bolin (1934, 1947) does not appear to be monophyletic; *A. meanyi* and *A. creaseri* should be placed separately. Clarification of the exact position of these two species in relation to *Icelinus* and *Myoxocephalus* and the *Artedius-Clinocottus-Oligocottus* group must await identification and examination of larvae of additional species of cottids and reexamination of adult characters.

TAXONOMIC DESCRIPTIONS

Larvae of *Artedius*, *Clinocottus*, and *Oligocottus* have been difficult to identify at both the specific and generic levels because of their striking similarities. Previous descriptions of larvae of this group have been inadequate to separate larvae at both the specific and generic levels because of inaccuracies or insufficient detail. Many of the diagnostic characters useful in separating these larvae are transient features which are present during only a part of larval development (e.g., head spines, nape bubble). Hence, frequently a combination of several characters is necessary for identification of the larvae. Therefore, to facilitate identification, larval descriptions are arranged in species groups formed by the shared presence of diagnostic characters (Table 3). This matrix table is based on a set of characters that will allow identification of the early life history stages of 13 species of *Artedius*, *Clinocottus*, and *Oligocottus*.

Larvae of *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, *A. Type 3*, *Oligocottus maculosus*, *O. snyderi*, *Clinocottus acuticeps*, *C. analis*, *C. embryum*, *C. globiceps*, and *C. recalvus* (Groups A, B, and C) are very similar in morphology, pigmentation, and spination. They are all relatively lightly pigmented with melanophores present on the nape, dorsolateral surface of the gut, and in a series on the ventral midline of the tail.

Presence and amount of head pigmentation varies within the group. All of these larvae possess blunt, rounded snouts, stubby bodies, and a bulging gut which trails somewhat below the rest of the body. These larvae are readily distinguished from all other known cottid larvae by the presence of multiple preopercular spines (> 5).

Larvae in Group A, *Artedius fenestralis*, *A. harringtoni*, *A. lateralis*, and *A. Type 3*, all have a distinctively stubby shape, a rounded snout, and a humped appearance in the nape region. They are further distinguished by a series of ventral midline melanophores posterior to the anus that extend onto the ventral finfold as characteristic pigment slashes in flexion and postflexion larvae. These *Artedius* larvae possess distinctive preopercular spination; postflexion larvae have a relatively high number (≥ 14) of preopercular spines. The dorsalmost, middle, and ventralmost spines are larger than the other spines creating the "Artedius" spine pattern unique to larvae of this group. Characters such as number of preopercular spines, number of ventral midline melanophores, size at formation of head pigmentation, presence of gut diverticula, and number of branchiostegal rays distinguish larvae of each species of *Artedius*.

Larvae in Group B are *Oligocottus maculosus* and *O. snyderi*. These larvae can be distinguished by the presence of a distinctive bubble of skin situated just anterior to the origin of the dorsal finfold in preflexion and early flexion larvae. Larvae of both species are more slender than larvae in Groups A and C and have a relatively short, compact gut. In contrast to larvae of Group A, the dorsalmost preopercular spine becomes larger than other spines in flexion and postflexion larvae. Characters useful in distinguishing larvae of the two species of *Oligocottus* are number and position of ventral midline melanophores, number of preopercular spines, number of parietal spines or prickles, and presence of melanophores on the nape bubble.

Group C includes *Clinocottus acuticeps*, *C. analis*, *C. embryum*, and *C. globiceps*. Larvae of *C. recalvus*, described by Morris (1951), also belong to Group C based on morphology. This is the least cohesive group in that larvae vary more in morphology and pigmentation than in the other groups. In general, larvae have a long gut, the posteriormost portion of which trails below the rest of the body. Larvae of all species except *C.*

TABLE 3. GROUPINGS OF *ARTEDIUS*, *CLINOCOTTUS*, AND *OLIGOCOTTUS* LARVAE BASED ON CERTAIN DIAGNOSTIC CHARACTERS.

Taxa	Preopercular spines*	"Arctidus" spine pat-tern†	"Clinocottus" spine pat-tern‡	Ventral midline melanophores	Branchiostegals	Gut diverticulae	Nape bubble	Hindgut diverticulae	Head pigment		Post-flexion	Nape pigment	Fin-fold pigment	Lateral pigment#
									Flexion	Pre-flexion				
A. <i>Arctidus fenestralis</i>	18-22	+	-	21-23	7	-	-	-	-	-	-	+	-	-
<i>Arctidus harringtoni</i>	18-22	+	-	13-19	6	+	-	-	-	-	-	+	-	-
<i>Arctidus lateralis</i>	14-16	+	-	22-31	6	+	-	-	+	+	+	+	-	-
<i>Arctidus</i> Type 3	22-24	+	-	9-13	6	+	-	-	-	-	-	+	-	-
B. <i>Oligocottus maculosus</i>	9-11	-	+	16-36§	6	-	+	-	-	+	+	+	-	-
<i>Oligocottus snyderi</i>	18-22	-	+	3-7	6	-	+	-	-	+/-	+/-	+	-	-
C. <i>Clinocottus acuticeps</i>	11-13	-	+	2-10	6	-	-	+	+	+	+	+	-	-
<i>Clinocottus analis</i>	9-11	-	+	16-22	6	-	-	+	+	+	+	+	-	+
<i>Clinocottus embryum</i>	13-14	-	+	15-21	6	-	-	-	-	-	+	+	-	-
<i>Clinocottus globiceps</i>	16-19	-	+	4-8	6 or 7	-	-	-	-	+	+	+	-	-
<i>Clinocottus recubus</i>	5-12	-	+	14-24	6	-	-	-	-	+	+	+	-	-
D. <i>Arctidus creaseri</i>	4	-	-	7-11	6	-	-	-	-	+	+	+	-	-
<i>Arctidus manayi</i>	4	-	-	8-13	6	-	-	-	-	+	+	+	-	+

* Number at height of development.

† Upper, middle, and lower preopercular spines largest.

‡ Upper preopercular spine largest.

§ Reared larvae from California and Oregon have 14-20 melanophores; reared larvae from British Columbia have 26-36 melanophores.

|| Based partially on Morris 1951.

In postflexion larvae.

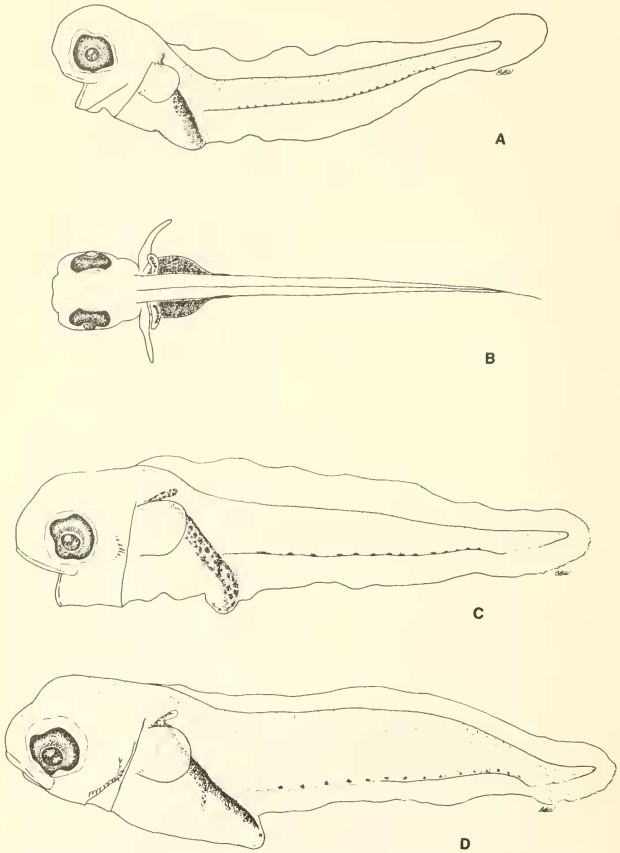


FIGURE 6. Larvae of *Artedius fenestralis*: A) 3.0 mm NL, B) 3.0 mm NL, C) 4.7 mm NL, D) 6.0 mm NL (from Richardson and Washington 1980).

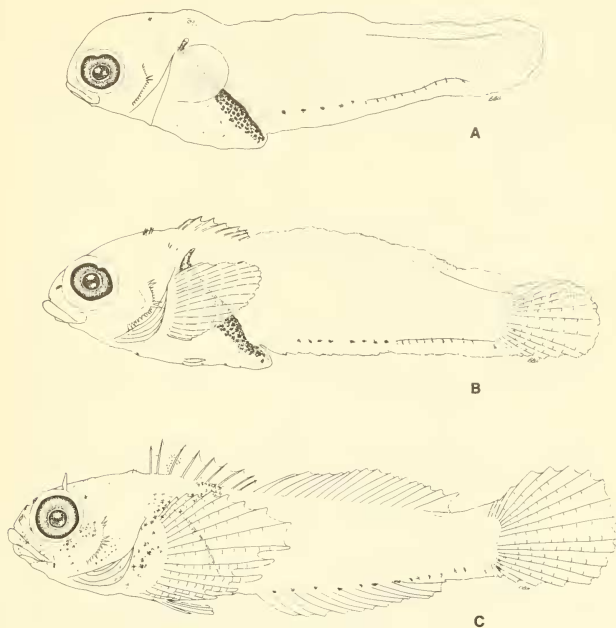


FIGURE 7. Larvae of *Artedius fenestralis*: A) 7.2 mm SL, B) 9.9 mm SL, C) 11.8 mm SL (from Richardson and Washington 1980).

embryum have melanistic pigmentation on the head and nape. The dorsalmost preopercular spine is larger than other preopercular spines in postflexion larvae. Characters such as number of preopercular spines, number and spacing of ventral midline melanophores posterior to the anus, and presence of hindgut diverticula or bulges are useful in separating larvae of each of these *Clinocottus* species.

Group D consists of *Artedius creaseri* and *A. meanyi*. These larvae differ from all other larvae of *Artedius*, *Clinocottus*, and *Oligocottus* species listed above in morphology, pigmentation, and spination. They have pointed snouts and large

heads, light pigmentation, and four preopercular spines. These characters bind them more closely with *Icelinus* larvae. In addition, *A. creaseri* and *A. meanyi* larvae are further distinguished by large blotch-like melanophores situated along the ventral midline posterior to the anus. Snout to anus length, meristics, finfold pigmentation, and nape pigmentation are useful characters in separating larvae of the two species.

Artedius fenestralis

(Figures 6–8; Table 4)

LITERATURE.—Blackburn (1973) illustrated an 8.5 mm SL larva similar to *Artedius fenestralis*,

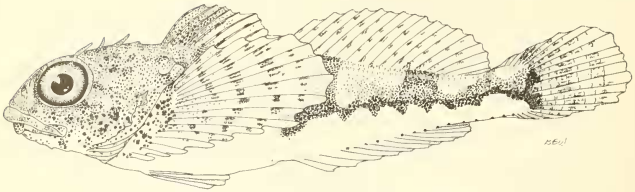


FIGURE 8. Juvenile of *Artedius fenestralis*, 19.1 mm SL.

which he described as Cottid 4. Eldridge (1970) and White (1977) briefly described and illustrated 3.2 mm and 3.9 mm larvae, respectively, which are similar to *A. fenestralis*. These illustrations also closely resemble *A. lateralis* larvae. Richardson and Percy (1977) listed these larvae as *Artedius* sp. 2. Richardson and Washington (1980) described and illustrated specimens 3.0, 4.7, 6.0, 7.2, 9.9, and 11.8 mm long as *Artedius* Type 2.

IDENTIFICATION.—Juveniles and adults were identified by the following combination of characters: high dorsal fin ray counts, absence of nasal and preorbital cirri, and the presence of scales on the head under the entire orbit and in a dense patch on the caudal peduncle. The developmental series was linked together primarily by pigmentation, body shape, gut diverticula, and preopercular and parietal spination. Identification of larvae was further confirmed through comparison with larvae reared from known eggs. Postflexion and transforming larvae were linked with juveniles using pigmentation, cirri patterns, spination, and meristics.

DISTINGUISHING FEATURES.—A combination of characters is useful in distinguishing preflexion *A. fenestralis* larvae including prominent gut diverticula protruding from the dorsal surface of the abdominal cavity, melanistic nape pigmentation, lack of head melanophores, and a series of 13–19 ventral midline melanophores posterior to the anus.

Late flexion and postflexion larvae are further distinguished by the presence of 18–22 preopercular spines with the dorsalmost, middle, and ventralmost spines being larger than the others. Postflexion larvae also have a cluster of 5 or 6

spines situated on the posterior margin of each parietal bone.

Juveniles of *A. fenestralis* are distinguished by meristics, dark pigmentation over the dorsolateral surface of the body, and 13–16 ventral midline melanophores posterior to the anus. Other useful characters include the absence of a nasal and preorbital cirrus, the presence of one or two small cirri on the eyeball, and two frontoparietal cirri.

PIGMENTATION.—Newly hatched larval *Artedius fenestralis* reared in the laboratory have no melanistic pigmentation on the head or nape. Intense melanophores are scattered over the dorsolateral surface of the gut. These lateral gut melanophores are frequently faded and difficult to see in field-collected larvae. Posterior to the anus, a series of 13–19 melanophores originates under the third or fourth postanal myomere and extends posteriorly along the ventral body midline. An additional 1 or 2 melanophores extend onto the ventral finfold near the notochord tip. These ventral midline melanophores are evenly spaced approximately one every other myomere.

During larval development, the head region remains unpigmented. Two to four melanophores are added on the nape in larvae 3.4 mm long and become embedded in musculature over the notochord by ~7 mm. By that size the posterior half of the series of ventral midline melanophores appear as distinctive slashes that extend onto the ventral finfold.

During transformation (planktonic specimens ~12–14 mm long) juvenile pigmentation begins to develop. Melanophores are added on the dorsal surface of the head, on the tip of the lower jaw, and on the pectoral fin base. Gradually, me-

TABLE 4. BODY PROPORTIONS OF LARVAE AND JUVENILES OF *ARTEDIUS FENESTRALIS*, *A. HARRINGTONI*, *A. LATERALIS*, AND *A. TYPE 3*. Values given are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses.

Item	<i>Artedius fenestralis</i>	<i>Artedius harringtoni</i>	<i>Artedius lateralis</i>	<i>Artedius Type 3</i>
Head length/SL:				
Preflexion	22.2 ± 1.41 (21.1–25.0)	20.9 ± 2.30 (18.7–22.3)	20.2 ± 2.68 (16.4–22.9)	21.8 ± 0.92 (20.7–23.2)
Flexion	22.1 ± 1.22 (20.3–23.3)	23.1 ± 3.86 (24.9–27.0)	23.6 ± 1.92 (19.9–26.1)	24.6 ± 1.71 (23.3–27.1)
Postflexion	26.1 ± 2.85 (20.8–29.4)	29.0 ± 0.50 (22.4–34.1)	26.9 ± 1.89 (24.3–30.8)	29.0*
Juvenile	33.9 ± 2.08 (32.0–34.9)	33.6 ± 3.46 (30.4–36.5)	22.7 ± 3.21 (19.1–25.3)	–
Snout length/HL:				
Preflexion	15.1 ± 3.77 (10.5–20.0)	18.9 ± 5.52 (9.9–25.1)	28.0 ± 1.83 (25.8–30.1)	19.8 ± 3.85 (15.4–24.6)
Flexion	20.4 ± 5.96 (12.3–26.6)	23.7 ± 6.14 (18.3–19.1)	25.2 ± 1.91 (22.9–29.4)	23.2 ± 3.51 (19.2–26.7)
Postflexion	21.8 ± 3.57 (17.5–24.5)	24.2 ± 4.19 (15.8–31.4)	24.7 ± 3.77 (19.4–30.6)	29.4*
Juvenile	21.6 ± 2.08 (19.8–23.2)	23.1 ± 1.00 (22.3–24.3)	23.0 ± 1.73 (18.9–24.7)	–
Eye diameter/HL:				
Preflexion	39.7 ± 4.32 (33.7–46.9)	44.7 ± 4.57 (39.7–50.1)	44.7 ± 2.87 (40.8–47.1)	46.7 ± 6.53 (39.0–57.6)
Flexion	41.2 ± 3.42 (37.4–46.5)	40.4 ± 7.33 (38.4–43.2)	40.4 ± 2.88 (37.4–45.5)	37.1 ± 2.16 (35.3–40.2)
Postflexion	36.9 ± 7.10 (27.3–52.1)	32.6 ± 4.09 (23.2–39.8)	36.6 ± 4.06 (37.9–44.6)	37.9*
Juvenile	29.1 ± 1.00 (24.6–27.3)	31.2 ± 5.77 (29.8–31.2)	35.3 ± 5.03 (22.1–24.8)	–
Snout to anus length/SL:				
Preflexion	45.3 ± 3.59 (41.2–50.8)	42.0 ± 3.21 (38.2–48.2)	40.4 ± 4.83 (33.3–45.6)	44.8 ± 2.76 (41.4–49.8)
Flexion	45.9 ± 2.49 (44.5–50.1)	47.3 ± 8.30 (36.5–55.9)	42.7 ± 3.65 (38.2–47.9)	45.1 ± 2.63 (43.2–48.1)
Postflexion	48.4 ± 2.26 (42.7–51.4)	49.9 ± 2.67 (45.9–55.4)	48.4 ± 2.18 (44.4–50.9)	50.2*
Juvenile	49.1 ± 2.00 (47.0–51.5)	47.4 ± 3.21 (43.1–49.2)	48.7 ± 4.04 (44.1–51.2)	–
Snout to pelvic fin origin/SL:				
Preflexion	–	–	–	–
Flexion	25.6 ± 3.21 (20.2–29.8)	–	–	25.3 ± 4.24 (21.9–27.6)
Postflexion	26.1 ± 3.21 (20.2–29.8)	27.8 ± 1.72 (24.5–30.8)	28.1 ± 3.11 (24.9–34.1)	29.3*
Juvenile	30.4 ± 3.51 (26.5–30.1)	27.4 ± 2.65 (24.1–29.4)	27.0 ± 3.61 (23.8–31.0)	–
Pelvic fin origin to anus/SL:				
Preflexion	–	–	–	–
Flexion	22.2 ± 5.35 (16.1–27.0)	–	–	23.1 ± 4.95 (19.1–26.1)
Postflexion	26.1 ± 3.21 (20.2–29.8)	22.8 ± 4.68 (17.2–34.8)	20.1 ± 4.20 (14.4–26.7)	20.9*
Juvenile	18.9 ± 1.15 (18.2–20.2)	19.9 ± 1.15 (18.9–21.3)	22.3 ± 2.08 (20.3–24.1)	–
Body depth at pectoral fin base/SL:				
Preflexion	21.7 ± 1.81 (19.0–23.8)	23.7 ± 2.99 (20.9–29.7)	23.0 ± 3.16 (17.9–26.3)	25.9 ± 1.77 (23.4–28.2)
Flexion	28.5 ± 2.70 (24.9–30.1)	28.1 ± 2.45 (28.0–31.2)	26.6 ± 2.33 (24.2–27.1)	28.2 ± 1.76 (26.3–30.1)
Postflexion	28.2 ± 1.82 (24.2–32.1)	30.5 ± 2.74 (23.4–34.1)	28.1 ± 2.29 (24.1–32.2)	30.0*
Juvenile	25.8 ± 1.53 (24.4–26.8)	22.3 ± 4.15 (24.6–25.2)	19.7 ± 3.06 (21.9–25.0)	–
Body depth at anus/SL:				
Preflexion	19.0 ± 2.49 (14.8–22.2)	27.8 ± 2.45 (17.2–27.6)	20.4 ± 2.51 (15.8–21.8)	22.9 ± 3.28 (18.2–27.2)
Flexion	24.1 ± 2.59 (23.6–27.1)	30.4 ± 3.32 (28.1–34.7)	26.3 ± 2.29 (24.5–31.3)	29.1 ± 2.06 (26.1–31.3)
Postflexion	27.9 ± 2.79 (21.4–32.8)	20.9 ± 5.77 (23.9–34.8)	26.3 ± 2.82 (22.4–33.0)	30.3*
Juvenile	21.6 ± 2.65 (18.9–24.4)	28.0 ± 1.72 (20.8–21.9)	30.3 ± 3.51 (17.4–22.8)	–
Pectoral fin length/SL:				
Preflexion	9.1 ± 0.98 (8.2–10.9)	7.4 ± 2.34 (4.4–11.1)	11.0 ± 1.08 (9.6–12.2)	10.4 ± 2.91 (7.1–13.3)
Flexion	9.4 ± 0.71 (8.4–10.4)	12.1 ± 3.54 (9.9–15.4)	12.3 ± 1.98 (9.6–15.9)	11.2 ± 3.50 (7.4–15.1)
Postflexion	22.6 ± 6.21 (9.7–29.7)	24.6 ± 7.59 (10.3–34.6)	19.8 ± 4.66 (13.3–27.6)	21.0*
Juvenile	26.2 ± 1.53 (27.1–28.4)	34.1 ± 3.61 (29.9–36.6)	30.3 ± 3.51 (26.8–34.2)	–

– = Not present at this stage.

* = Only one specimen available in this stage.

lanophores develop on the anteriormost portion of the spinous dorsal fin, then extend ventrally as a band of pigment stretching from the fourth or fifth dorsal spine to the pigmentation over the dorsal surface of the gut just posterior to the pectoral fin base.

Juvenile pigmentation increases markedly in newly settled individuals 13 mm SL. Numerous melanophores are added over the dorsolateral surface of the head and become concentrated in the parietal-interorbital region. Additional melanophores extend down onto the snout and lips. Laterally, melanophores are added in the cheek region between the eye and the preopercle and the dorsal portion of the opercle. Several melanophores are clustered at the posterior edge of the lower jaw. The ventral surface of the head remains unpigmented. Pigmentation gradually extends from the head posteriorly across the dorsolateral surface of the body until it fuses with bands of pigment reaching from the middle of the spinous dorsal fin to the gut. Pigmentation increases on the anterior end of the dorsal fin creating a dark blotch of pigment across the first four dorsal spines. Melanistic pigmentation also increases on the pectoral fin base with melanophores extending onto the pectoral fin rays and eventually forming several bands of pigmentation. Several irregular clusters of melanophores appear along the lateral midline and gradually form a band of pigment reaching from the gut to the caudal peduncle.

As juvenile pigmentation develops, saddles of pigment form along the dorsum in an anterior to posterior sequence. The first saddle or band of pigment forms under the 4th–7th dorsal fin rays. Gradually, melanophores extend ventrally from the pigment saddle and merge with the lateral midline melanophores. Concurrently, a second saddle of pigment forms under the 9th–10th dorsal fin rays, while a third saddle of pigment begins to develop under the 13th–15th dorsal fin rays. Melanophores from these pigment saddles also extend ventrally and fuse with the lateral midline pigment. At the same time, melanophores are added on the dorsal fin forming three to four bands. Melanophores extend ventrally from the lateral midline band and form a series of five to eight scallops which reach just below the lateral midline. The rest of the ventrolateral surface of the body remains characteristically unpigmented until juveniles reach about 19–20 mm. As the dorsal pigment saddles are forming, the

lateral midline melanophores extend posteriorly to the base of the caudal fin where they form a dark band. Gradually, melanophores extend onto the caudal fin rays forming three or five indistinct bands of pigment. Approximately 13–16 ventral midline melanophores remain visible in juveniles up to ~20 mm long.

MORPHOLOGY.—Larvae of *Artedius fenestralis* hatch at ~3.5–3.8 mm NL. Flexion of the notochord occurs between 5.9 and 6.8 mm NL. The largest planktonic larva collected is 13.9 mm and is beginning to undergo transformation. The smallest benthic juvenile examined is 13.1 mm. Thirty-four selected specimens, 3.2–21.2 mm, were examined for developmental morphology.

Larval *A. fenestralis* have stubby bodies with a humped appearance in the nape region. Distinctive diverticula extend dorsolaterally from the dorsal surface of the gut just posterior to the origin of the pectoral fin base. These diverticula are present in newly hatched larvae and remain prominent in the largest planktonic larvae. The diverticula completely disappear in benthic juveniles shortly after settling. The gut itself is moderately long and the posterior portion of the hindgut trails well below the rest of the body. Snout to anus length increases from 43% to 45% SL during larval development, then increases to 49% SL in benthic juveniles. *Artedius fenestralis* larvae have a short, rounded snout with snout length increasing from 15% HL in preflexion larvae to 23% HL in postflexion larvae and juveniles.

FIN DEVELOPMENT.—Caudal fin rays begin to form at ~6 mm. The adult complement of principal caudal rays is present in larvae ~7 mm long. The bases of the dorsal and anal fin rays appear in 7–7.5 mm larvae. The full complement of fin rays is formed by ~8.5–9 mm. Dorsal fin spines begin to form at ~8 mm, and the full complement of spines (VIII–IX) is present by ~9.5 mm. Although pectoral fin rays are visible by ~7 mm, the adult complement (14–16) is not formed until ~9 mm. Pelvic buds form between 6.5 and 7 mm and the adult complement of 1.3 pelvic fin rays is formed in larvae ~10 mm long.

SPINATION.—Seven to 13 tiny spines begin to form along the posterior margin of the preopercle in larvae ~4.7 mm NL. The preopercle appears to develop in two arc-shaped sections, which overlap slightly at the angle of the preopercle. Three to 7 spines are present along the dorsal-most section and 6–8 spines occur on the lower

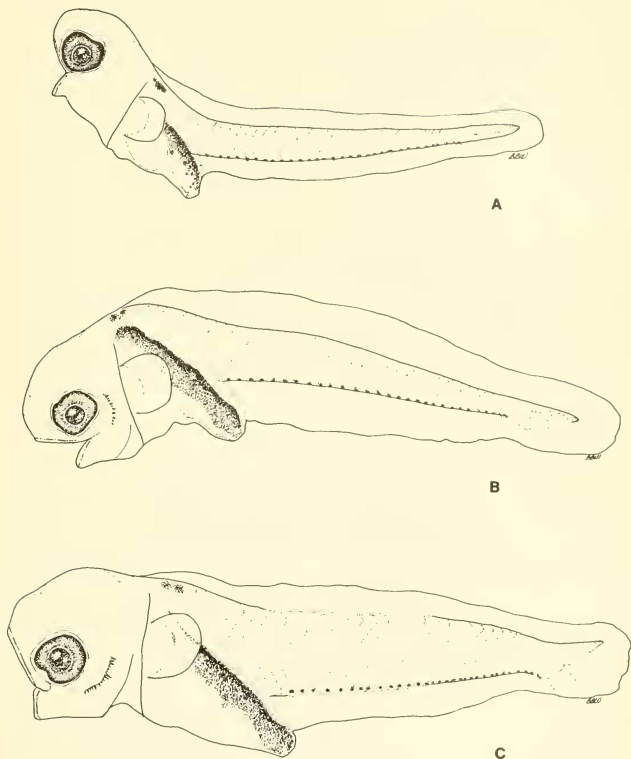


FIGURE 9. Larvae of *Artedius harringtoni*: A) 3.0 mm NL, B) 4.7 mm NL, C) 6.9 mm NL (from Richardson and Washington 1980).

section. The two sections fuse together in post-flexion 7 mm long. Two spines located at the site of fusion begin to increase in length relative to the other preopercular spines. Concurrently, the preopercular spines increase in number during larval development and range between 18 and

21 in larvae >8 mm long. The dorsalmost and middle two spines continue to increase in size relative to the other spines, becoming nearly three times as long. The ventralmost 2 or 3 spines also increase in size, becoming 1.5 to 2 times as long as the other spines. The number of preopercular

spines decreases in transforming larvae > 13 mm long. The smaller spines (4-6, 8-10, and 13-15) begin to regress first. Newly settled juveniles possess one large dorsal preopercular spine. The lower spines are visible only as serration, or bumps, on the preopercular margin. The dorsalmost spine continues to increase in size while the lower bumps eventually disappear in juveniles ~19 mm long.

Clusters of spines also develop in the parietal and supracleithral-posttemporal regions. One or two spines form at the posterior end of the parietal in larvae ~6 or 7 mm long. A third spine is added in 7-8-mm larvae. Larvae > 8 mm have four to six spines located in two rows on each side of the head. Usually, three spines occur in the anterior row while two or three spines are present in a second row posterior to and parallel to the first row. These spines begin to regress in size in transforming larvae > 12-13 mm long. The anterior spines curve posteriorly, eventually fusing with spines from the posterior row forming a hollow arch and canal. This canal develops into part of the cranial lateral line system in juveniles ~14-15 mm long.

Two small spines develop on the ventral portion of the posttemporal in larvae 6-7 mm long. A third spine is added on the posttemporal in larvae > 8 mm long. Concurrently, another spine develops on the dorsal tip of the supracleithrum. These spines remain prominent in planktonic larvae ≤ 12 mm long; however, in transforming juveniles the spines gradually curve dorsally and ventrally and fuse together forming a bony tube or canal. This canal becomes the anteriormost juncture of the lateral line and cephalic lateral line systems in juveniles.

Artedius harringtoni

(Figures 9-11; Table 4)

LITERATURE.—Blackburn (1973) described a 4.6 mm larva that he called Cottid 6 that is similar to *A. harringtoni*. Richardson and Washington (1980) illustrated and described specimens 3.0, 4.7, 6.9, 7.3, 9.3, and 13.6 mm long.

IDENTIFICATION.—Juveniles and adults were identified primarily on the basis of the following characters: high dorsal fin ray counts (16-18), low pectoral fin ray counts (usually 14), presence of seven branchiostegals, presence of a preorbital cirrus, scales extending onto the head under only the posterior portion of the orbit, and scales ab-

sent on the snout. The developmental series of larvae was linked together by pigmentation, preopercular spination, absence of gut diverticula, body shape, and the possession of seven branchiostegals. Postflexion and transforming larvae were linked with juveniles primarily on the basis of pigmentation, meristics, and presence of a preorbital cirrus.

DISTINGUISHING FEATURES.—Characters useful in distinguishing small larval *A. harringtoni* are a combination of presence of melanistic nape pigment, lack of head pigmentation, a series of 21-33 pigment slashes along the ventral midline of the tail, and a humped appearance in the nape region. Absence of dorsal gut diverticula distinguishes larval *A. harringtoni* from similarly pigmented larvae of *A. lateralis*, *A. fenestralis*, and *A. Type 3*.

Postflexion larvae 6.5 mm are distinguished by the presence of 18-22 spines along the posterior margin of the preopercle. The dorsalmost and middle preopercular spines are characteristically larger than the other spines. Larvae > 7 mm have seven branchiostegal rays. Larvae of all other species of *Artedius* have only six branchiostegal rays.

Juvenile *A. harringtoni* may be recognized by the dark pigmentation over the head and nape, possession of seven branchiostegals, retention of 18-22 ventral midline melanophores, possession of a preorbital cirrus, and dorsal and pectoral fin ray counts.

PIGMENTATION.—Preflexion larvae have no melanistic pigmentation on the head; however, 3-5 small, external melanophores are concentrated in a dense patch on the nape. The dorsolateral surface of the gut is covered with numerous large, intense melanophores. One to 8 tiny melanophores encircle the anus. Posterior to the anus, the only pigmentation consists of a series of 23-33 melanophores positioned along the ventral midline. This series originates under the first to third postanal myomere and extends posteriorly toward the tail tip with 1 or 2 melanophores positioned under each myomere. An additional 1 to 3 melanophores frequently occur on the caudal finfold near the tail tip.

During larval development the head region remains unpigmented. The nape melanophores become embedded in the musculature over the notochord in larvae > 7 mm. Concurrently, the number of ventral midline melanophores decreases to between 21 and 30, and the posterior

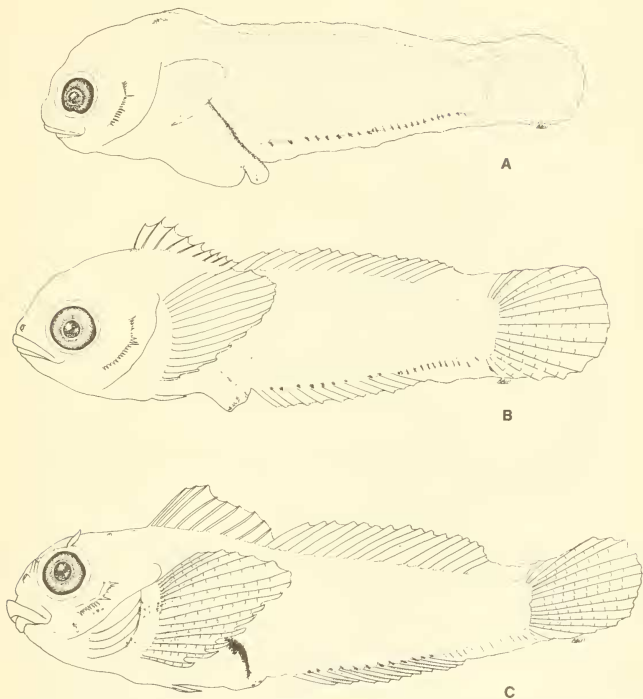


FIGURE 10. Larvae of *Artedius harringtoni*: A) 7.3 mm SL, B) 9.3 mm SL, C) 13.6 mm SL (from Richardson and Washington 1980).

half of the series appears as characteristic pigment slashes that extend onto the ventral finfold.

During transformation, planktonic larvae > 10 mm begin to develop juvenile pigmentation. Melanophores are added on the tip and base of the lower jaw, on the cheek between the eye and the dorsalmost preopercular spine, on the operculum, and on the isthmus.

Pigmentation increases markedly over the head

in newly settled benthic juveniles. Melanophores develop on the snout and upper lip and on the dorsal surface of the head over the brain. Melanophores gradually extend posteriorly from the head and eventually join with the nape pigmentation. Concurrently, melanophores extend posteroventrally from the posttemporal region toward the dorsal gut pigment. Numerous large melanophores form over the base of the pectoral

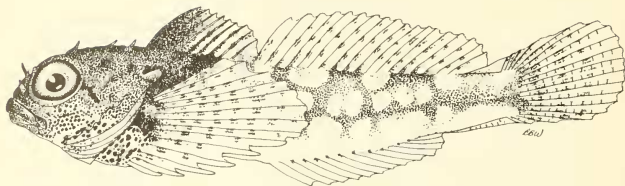


FIGURE 11. Juvenile of *Artedius harringtoni*, 13.9 mm SL.

fin, and subsequently extend onto the pectoral fin rays forming four or five distinct pigment bands across the fin. A band of melanophores also extends ventrally from the pectoral fin base and covers the isthmus.

In juveniles >13 mm long, the entire head is heavily pigmented. Melanophores extend posteriorly from the head to a vertical line under the seventh dorsal fin spine. A dense patch of melanophores develops at the anterior end of the spinous dorsal fin forming a dark blotch across the fin membrane between the first four dorsal spines. Scattered melanophores are added along the rest of the dorsal fin eventually forming three or four bands of pigment.

Posterior to the head, pigmentation is added in three saddles along the dorsum. The first saddle of pigment forms under the 2nd–4th dorsal fin rays, the second saddle forms under the 7th–10th dorsal fin rays, and the third forms under the 13th–15th fin rays. Concurrently, an irregular band of faint melanophores develops along the lateral midline. This lateral pigmentation gradually extends posteriorly from the abdominal region to the caudal peduncle. As development proceeds, bands of melanophores extend ventrally from each of the saddles on the dorsum and merge with the lateral midline pigment. As a result, the dorsolateral surface of the tail is covered by bands of pigmentation, which enclose small unpigmented saddles and circles creating a characteristic pattern.

Subsequently, groups of melanophores extend ventrally from the lateral midline pigmentation creating a scalloped edge of pigment along the ventrolateral body surface. Eventually, melanophores from the tips of each scallop extend laterally and join together enclosing four to six distinctive unpigmented circles, characteristic of juvenile *A. harringtoni*.

In late stages of juvenile pigmentation, the lateral band of melanophores extends posteriorly to the base of the caudal fin. Melanophores are added on the caudal fin rays forming five to seven bands of pigmentation.

Between 18 and 21 ventral midline melanophores remain visible in juveniles <15 mm.

MORPHOLOGY.—The smallest *A. harringtoni* larva from plankton collections is 3.0 mm NL and still retains remnants of its yolk. Larvae undergo flexion of the notochord between 5.2 and 6.4 mm NL. The largest planktonic larva examined is 13.6 mm long and beginning to undergo transformation. The smallest benthic juvenile collected in tidepools is 12.9 mm and is just beginning to develop juvenile pigmentation on the head and pectoral fin base. Thirty-five selected specimens, 3.0–13.7 mm, were examined for morphometrics.

Larvae of *A. harringtoni* are stubby with a distinctive humped appearance in the nape region. Unlike larval *A. fenestralis*, *A. lateralis*, and *A. Type 3*, larval *A. harringtoni* have no dorsal gut diverticula. The gut is moderately long with snout to anus length ranging from 42% in preflexion larvae to 50% SL in postflexion larvae. Relative snout to anus length decreases slightly in benthic juveniles. The hindgut appears to trail below the rest of the body. Relative body depth at the pectoral fin base increases from 23% in preflexion larvae to 30% in flexion and postflexion larvae.

Artedius harringtoni have blunt heads and rounded snouts. Head length increases relative to body length during development, averaging 21% in preflexion larvae, and 34% SL in juveniles. Snout length increases from 19% to 22% HL during larval development.

FIN DEVELOPMENT.—A thickening in the hypural region of the developing caudal fin is first visible at 4.7 mm NL, just prior to the onset of

notochord flexion which occurs at ~5.2 mm NL. Caudal fin rays begin to form in larvae ~6 mm; however, the adult complement of principal caudal rays is not complete until larvae reach ~7 mm long.

Bases of the dorsal and anal fin rays form in larvae ~6–7 mm long. Dorsal spines begin to form in larvae ~7–8 mm long. The adult complement of dorsal and anal fin rays is complete at 9.3 mm. Pectoral fin rays are first visible between 6 and 7 mm, and the adult complement (13–15) is countable at ~7.5 mm. The pelvic fin bud begins to form at ~7.1 mm, and the adult complement of I,3 is complete by ~10 mm.

SPINATION.—Eight to ten tiny spines begin to form along the posterior margin of the preopercle in larvae ~4.5 mm NL. The number of spines increases to 18–22 in flexion and postflexion larvae. By the end of flexion, ~6.7 mm, the middle two spines (7–9) begin to increase in size relative to the other preopercular spines. In larvae >7.5 mm, the dorsalmost two or three spines also increase in size relative to other spines. As development proceeds, the dorsalmost and middle spines increase in length and diameter creating a characteristic pattern with small, inconspicuous spines situated between the dorsalmost and middle spines, and ventral to the middle spines. In larvae >8.5 mm, the ventralmost four or five spines also become somewhat larger than the spines directly above them. When larvae reach ~10–11 mm SL, the preopercular spines begin to regress with the small, inconspicuous spines disappearing first. At the onset of transformation (~12–13 mm) only four spines remain in the approximate position of the original spines (1–2, 4–9, 12–14, and 18–22). In newly settled juveniles, the dorsalmost preopercular spine becomes quite long and stout while the lower three spines gradually become smaller and visible only as slight bumps on the margin of the preopercle.

Spines never develop in the parietal and post-temporal region of the head. However, in cleared and stained larvae, bony thickenings are visible in the parietal region at the same position as parietal spines found in other cottid larvae.

Arteidius lateralis

(Figures 12, 13; Table 4)

LITERATURE.—Budd (1940) described and illustrated a newly hatched larva of *A. lateralis* 4.1 mm TL. Marliave (1975) described larvae of *A. lateralis* and illustrated specimens 4 mm TL, 8 mm TL, 11 mm TL, and 14 mm TL long.

IDENTIFICATION.—Small larval *A. lateralis* were reared from eggs spawned from known adults. Juveniles and adults were identified using the following characters: pigmentation, absence of scales on the head and caudal peduncle, absence of nasal and preorbital cirri, and the presence of 3–11 scales in the longest row in the dorsal scale band. The developmental series was linked together primarily on the basis of pigmentation, preopercular spination, presence of gut diverticula, and body shape. Postflexion and transforming larvae were linked to juveniles by pigmentation, cirri patterns, spination, and meristics.

DISTINGUISHING FEATURES.—Characters useful in distinguishing preflexion larvae of *Arteidius lateralis* are prominent diverticula which extend dorsolaterally from the dorsal surface of the gut just posterior to the pectoral fin bases, the lack of head and nape pigment in larvae <6 mm NL, and a series of 22–32 melanophores that lie along the ventral midline posterior to the anus. The anterior half of the series is characterized by one large melanophore per myomere while the posterior half of the series consists of two or three smaller pigment slashes per myomere.

Postflexion larvae of *A. lateralis* >6.2 mm can be distinguished from other *Arteidius* larvae by melanistic pigmentation over the brain. Juvenile *A. lateralis* are distinguished by two dark bars of melanophores extending ventrally from the dorsal fins across the lateral surface of the body trunk, the series of 11–21 ventral midline melanophores, and meristics.

PIGMENTATION.—Newly hatched larvae of *A. lateralis* have no melanistic pigmentation on the head or nape. Dense, round melanophores are concentrated over the dorsolateral surface of the gut and extend dorsally onto the gut diverticula. A cluster of 4 to 6 small melanophores surrounds the anus. Posterior to the anus, a series of 22–32 melanophores lies along the ventral midline of the body. These melanophores originate under the third or fourth postanal myomere and extend posteriorly toward the tail tip where several additional melanophores extend onto the caudal finfold. Melanophores in the anterior half of this series are relatively large and spaced one per myomere. The posteriormost melanophores appear as small pigment slashes, which extend onto the ventral finfold and are closely spaced two or three to every myomere.

During larval development, melanophores form on the dorsal surface of the head in larvae >6.3 mm. Two to five melanophores also form

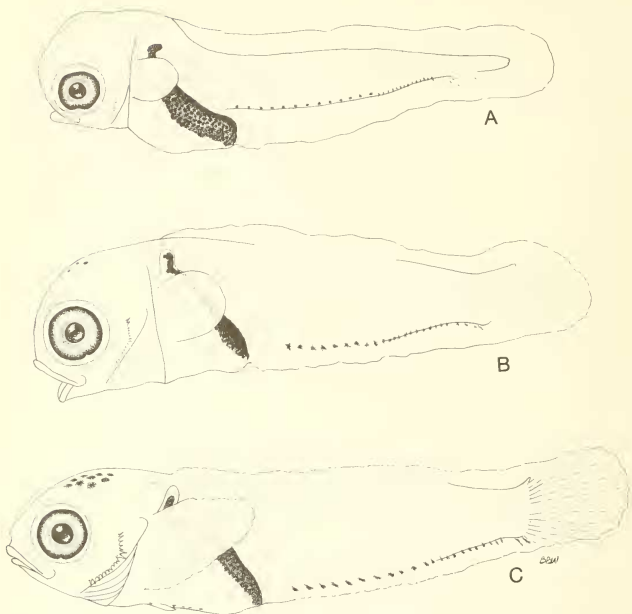


FIGURE 12. Larvae of *Arctidius lateralis*: A) 4.6 mm NL, B) 6.4 mm SL, C) 7.1 mm SL.

at the base of the cleithrum and along the ventral midline of the gut in larvae > 5.2 mm. These melanophores are arranged in a characteristic T shape with two melanophores positioned as horizontal slashes at the base of the cleithrum and one to three melanophores extending posteriorly along the ventral midline of the gut.

During transformation, in planktonic larvae > 8 mm, melanistic pigmentation increases markedly on the dorsal surface of the head with 33–44 dark melanophores covering the brain. Melanophores also form just posterior to the lower jaw, on the cheek between the eye and the preopercle and on the operculum. Ventral mid-

line melanophores remain unchanged in number and spacing.

Pigmentation increases markedly in newly settled juveniles > 10 mm long. Dark melanophores form on the dorsolateral surfaces of the head and extend anteriorly onto the snout and upper and lower lips. Several melanophores are added to the gular region beneath the lower jaw. Intense pigment forms on the bases of the pectoral fins and several large melanophores extend onto the pectoral fin rays. Gradually, melanophores from the base of the pectoral fin extend ventrally forming a band of pigment across the isthmus. With development, pigmentation increases on the head

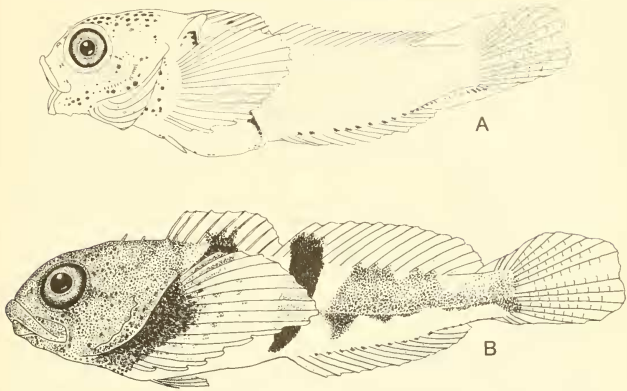


FIGURE 13. Young of *Artedius lateralis*: A) 9.1 mm SL, B) 13.3 mm SL.

so that in larvae ≥ 12 mm SL, the entire head is darkly pigmented.

Shortly after settling, in larvae between 10 and 11 mm, a patch of melanophores is added to the dorsal fin between the fourth and sixth spines. These melanophores extend ventrally across the dorsum toward the pigmentation on the pectoral fin base. A second band of melanophores forms on the second dorsal fin membrane between the 2nd and 4th fin rays. Gradually this band extends anteroventrally below the lateral midline. With development, the two vertical bands of pigment become very dark and intense. Melanophores from these bands extend dorsally across the dorsal fins. Concurrently, three saddles of faint melanophores are added posteriorly along the dorsum. The first saddle of pigment forms under the 8th–10th dorsal fin rays, the second saddle is added under the 12th–15th fin rays, and the third saddle forms on the dorsal surface of the caudal peduncle. Gradually, melanophores from these pigmented saddles extend ventrolaterally and join together forming a band along the lateral midline. Lateral pigmentation extends posteriorly and forms a band along the base of the caudal fin. Melanophores extend onto the caudal fin rays,

gradually forming two or four distinct bands across the caudal fin. Ventral midline melanophores decrease in number in juveniles from 11 to 21. These melanophores remain visible in juveniles < 15 mm long.

MORPHOLOGY.—*Artedius lateralis* larvae are 3.9–4.5 mm long at hatching. Flexion of the notochord occurs between 5.0 and 6.3 mm NL. The largest planktonic specimen observed is 9.2 mm and beginning to develop juvenile pigmentation. *A. lateralis* settle at a relatively small size, ~9.5 to 10.5 mm. Thirty-three specimens (4.1–12.1 mm) were examined for developmental morphometrics.

Larvae of *A. lateralis* are rather stubby with a moderately short gut. Snout to anus length averages 40% in preflexion larvae, then increases to 48% SL in postflexion larvae and juveniles. Pronounced diverticula extend dorsally from each side of the gut just posterior to the pectoral fin base. The diverticula are present in newly hatched larvae and remain prominent throughout larval development. Tiny remnants of the diverticula are present in newly settled juveniles between 9 and 10.5 mm long.

Larvae of *A. lateralis* have a long rounded snout

relative to other *Artedius* Group A larvae. Snout length decreases from 28% to 24% HL during larval development.

FIN DEVELOPMENT.—The notochord begins to flex in larvae ~5 mm long, and is fully flexed in larvae between 5.7 and 6.3 mm. Caudal rays begin to form during flexion in larvae ~5.5 mm; however, the adult complement of 6 + 6 principal caudal rays is not complete until ~6 mm. Bases of the dorsal and anal fins are first visible in larvae between 6 and 6.5 mm and the adult complement of dorsal (15–17) and anal (12–14) rays is complete by about 7.5–8 mm.

Pectoral fin rays begin to form between 7 and 8 mm, but the full complement of rays (14–16) is not formed until larvae are ~8 mm long. Pelvic fin buds are first visible in a 7.4 mm larva; however, the fin rays are not countable until 9 mm.

SPINATION.—In preflexion larvae ~4.5 mm NL 8–9 tiny spines are visible on the posterior margin of the preopercle. As larvae undergo flexion of the notochord, the number of preopercular spines increases to 9–14. By the end of flexion, larval *A. lateralis* have 14–16 preopercular spines. In larvae > 7 mm, the dorsalmost and middle (spines 6–9 from the top of the preopercle) become slightly longer than the other preopercular spines. These spines never become more than 1.5 times larger than the other preopercular spines, in contrast to the situation in larvae of *A. harringtoni*, *A. fenestralis*, and *A. Type 3* in which the dorsalmost and middle preopercular spines may be nearly 2.5 times larger than the other spines. Preopercular spines begin to regress in transforming specimens > 9 mm. The dorsalmost spine increases in size while the lower spines (4–6 and 9–12) decrease in size becoming visible only as small serrations or irregularities on the preopercular margin. Spines 7–8, 12–13, and 16–18 fuse together to form blunt bumps along the preopercular margin. In juveniles > 13 mm, only the large, dorsalmost spine remains. Transforming larvae reared in the laboratory possess 4–5 small spines at the posterior margin of the parietals. These spines are not present in planktonic larvae from field collections, nor are they visible in newly settled juveniles from tidepools.

Artedius Type 3

(Figures 14, 15; Table 4)

LITERATURE.—Larvae of *Artedius* Type 3 have not been previously described.

IDENTIFICATION.—Only a partial size series (2.9–7.6 mm) of *Artedius* Type 3 larvae are available, all from California collections. The presence of prominent gut diverticula and the characteristic *Artedius*-type preopercular spine pattern (dorsalmost, middle, and ventralmost spines larger than the others) identifies this larval type as an *Artedius*. Larvae remain unknown for only two species of *Artedius*, *A. corallinus* and *A. notospilotus*. Meristics of the largest larva of *Artedius* Type 3 coincide with those recorded for both *A. corallinus* and *A. notospilotus*. However, pectoral counts fit those of *A. notospilotus* most closely. The 7.6 mm larval *A. Type 3* possesses 16 pectoral fin rays. Ninety % of the *A. notospilotus* examined by Howe and Richardson (1978) possessed 16 pectoral fin rays while only 10% of *A. corallinus* specimens possessed 16 pectoral fin rays.

Pigmentation along the ventral midline posterior to the anus of *A. Type 3* larvae (9–13 widely spaced melanophores) coincides most closely with that of juvenile *A. corallinus*. Several *A. corallinus* 13.5–14 mm long, possess 3–6 widely spaced ventral midline melanophores. In contrast, a 16-mm juvenile *A. notospilotus* possesses 24 ventral midline melanophores spaced one every one or two myomeres.

Adult *A. corallinus* are common in the intertidal areas of the southern California coast where *Artedius* Type 3 larvae were collected (Miller and Lea 1972). *Artedius notospilotus* adults are rare in the same area.

Additional larger specimens are needed before larvae of *Artedius* Type 3 can be specifically identified.

DISTINGUISHING FEATURES.—*Artedius* Type 3 larvae are distinguished as an *Artedius* by the distinctive diverticula that extend dorsolaterally from the dorsal surface of the gut just posterior to the pectoral fin base. *Artedius* Type 3 larvae are distinguished from small larvae of *A. fenestralis*, which possess similar diverticula, by the low number (9–13) of ventral midline melanophores posterior to the anus. Other characters useful in distinguishing small *A. Type 3* larvae are absence of head pigmentation and presence of a cluster of 2–4 melanophores in the nape region. Preopercular spines begin to form in larvae < 4.1 mm NL. Preopercular spines do not form in other *Artedius* larvae with multiple preopercular spines until ~4.5 mm NL. Flexion and postflexion larval *Artedius* Type 3 possess 21–

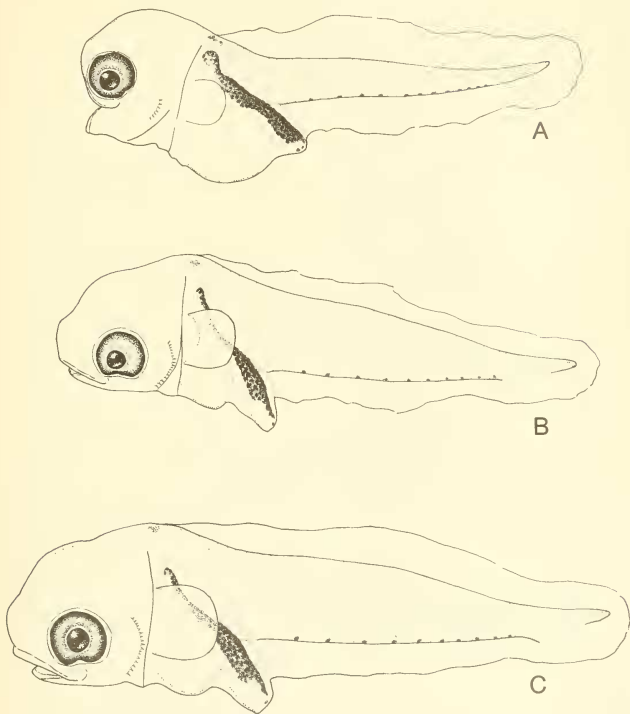


FIGURE 14. Larvae of *Artedius* Type 3: A) 3.2 mm NL, B) 4.1 mm NL, C) 4.9 mm NL.

24 preopercular spines, more than other larval *Artedius* (groups A and D), all of which have ≤ 21 preopercular spines.

PIGMENTATION.—Small preflexion larvae of *Artedius* Type 3 possess no melanistic head pigmentation. Two to four small external melanophores are clustered on the surface of the nape. Numerous dark, rounded melanophores are concentrated over the dorsolateral surface of the gut

and extend dorsally onto the gut diverticula. One to four small melanophores are clustered around the anus.

Posterior to the abdominal cavity, the only pigmentation consists of a series of 9–13 melanophores located along the ventral midline. This series of melanophores originates under the third to fourth postanal myomere and extends posteriorly toward the tail tip. Each melanophore is

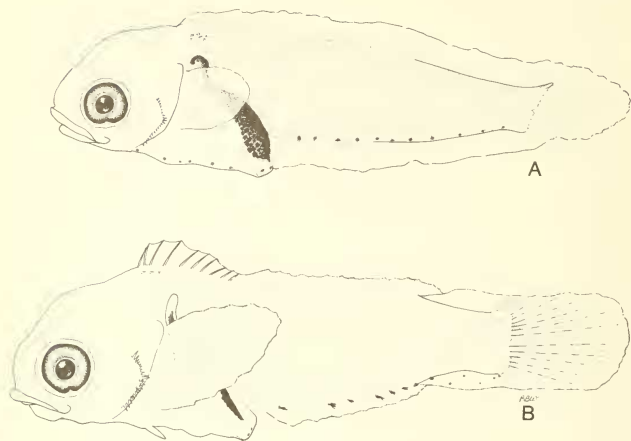


FIGURE 15. Larvae of *Artedius* Type 3: A) 6.8 mm SL, B) 7.3 mm SL.

spaced approximately two to three myomeres apart. An additional one to five pigment slashes extend onto the caudal finfold near the tail tip.

Pigmentation changes little during larval development. Melanophores are added in the nape region and become embedded in the musculature over the notochord in larvae <5.5 mm. Melanophores are also added in the isthmus region and along the ventral midline of the gut.

MORPHOLOGY.—The smallest larval *Artedius* Type 3 is 2.9 mm NL and possesses remnants of the yolk sac. Larvae undergo flexion of the notochord between 5.6 and 6.9 mm NL. The largest specimen examined is 7.6 mm long and has recently completed notochord flexion. Size at transformation is unknown. Thirteen larvae (2.9–7.6 mm long) were examined for developmental morphology.

Larvae of *Artedius* Type 3 are rather stubby with a moderately long gut; the posteriormost portion of this gut trails somewhat below the rest of the body. A prominent diverticulum extends dorsally from each side of the gut just posterior to the base of the pectoral fin. Diverticula are present in the smallest larva examined (2.9 mm

NL) and remain pronounced in the largest specimen.

Snout to anus length averages 45% SL in both preflexion and flexion larvae. Body depth at the pectoral fin base increases during development from 26% in preflexion larvae, to 28% in flexion larvae, and 32% SL in the single postflexion larva. Relative body depth at the anus also increases with development, from 23 to 30% SL. The distances from the snout to the origin of the pelvic fins and from the origin of the pelvic fins to the anus averages 26 and 22% SL, respectively, in late flexion and early postflexion larvae.

Artedius Type 3 larvae have a rather large head with a blunt, rounded snout. With development relative head length increases from an average of 22% in preflexion larvae to 25% in larvae undergoing flexion of the notochord, and 29% SL in the postflexion larva. Jaw length averages about 43% HL throughout early larval development. In contrast, eye diameter decreases during development from an average of 47% in preflexion larvae to 37% HL in flexion and early postflexion larvae.

FIN DEVELOPMENT.—A 4.9-mm NL larva ex-

hibits a slight thickening of the hypural region of the forming caudal fin. By 5.6 mm, the notochord of larval *A.* Type 3 is strongly flexed and caudal rays are beginning to form. Notochord flexion is nearly complete by ~7 mm and the adult complement (6 + 6) of principal caudal rays is countable.

The dorsal and anal fin bases are first visible in larvae between 6.8 and 6.9 mm long. In the largest specimen examined, 7.6 mm, the adult complement of dorsal spines (IX), dorsal rays (13–15), and anal fin rays (12) is complete. Pectoral fin rays begin to form in a larva 6.8 mm NL, and 16 pectoral fin rays are countable in a larva 7.6 mm. Pelvic fin buds are first visible at ~6.8 mm NL; however, pelvic fin rays are not yet formed in the largest specimen.

SPINATION.—Preopercular spines begin to form in small preflexion larvae of *A.* Type 3 at ~4.1 mm NL. A series of 15–17 tiny, equal-sized spines is visible along the posterior margin of the opercle in preflexion larvae between 4.1 and 5 mm NL. During development, preopercular spines increase in number ranging from 21 to 24 in flexion and early postflexion larvae.

In late flexion larvae (~6.8–6.9 mm NL) the middle 2 or 3 preopercular spines (the 8th–11th spine from the dorsal margin of the opercle) begin to increase in size relative to other preopercular spines. In the 7.6-mm larva, the dorsalmost and ventralmost 1 or 2 spines are also larger than other preopercular spines. This forms the characteristic preopercular spine pattern found in *Arteidius* larvae with multiple preopercular spines: the dorsalmost, middle, and ventralmost spines are markedly larger than the other preopercular spines.

No other spines develop on the head in larvae ≤7.6 mm. Head spination in larger larvae remains unknown.

Oligocottus maculosus

(Figures 16, 17; Table 5)

LITERATURE.—Stein (1972, 1973) described *O. maculosus* larvae and illustrated specimens 4.6, 6.0, 6.6, and 9.2 mm TL.

IDENTIFICATION.—Larvae in this series were reared from eggs spawned from known adults. Adults and juveniles were identified by the following combination of characters: high vertebral (33–34) and dorsal fin ray (15–18) counts, small size at transformation (8–9 mm), absence of cirri

on the nasal spines and along the base of the dorsal fins, and pigmentation. The developmental series was linked together primarily on the basis of pigmentation, preopercular and parietal spination, and body shape. Postflexion and transforming larvae were linked to juveniles by the serial method utilizing pigmentation, spination, and size at transformation.

DISTINGUISHING FEATURES.—Newly hatched larvae of *O. maculosus* reared in the laboratory are distinguished by the following pigmentation characters: intense melanistic nape pigment, dark dendritic melanophores that extend onto a prominent bubble of skin in the nape region just anterior to the origin of the dorsal finfold, 1 or 2 melanophores situated anteriorly on the visceral mass beneath the pectoral fins, and a series of 18–36 ventral midline melanophores posterior to the anus. In addition to distinctive pigmentation, larvae possess two rounded humps or protrusions that extend dorsally on either side of the gut just posterior to the pectoral fin bases. These protrusions are similarly positioned and reminiscent of the gut diverticula found in larvae of *Arteidius*; however, they never develop into distinct diverticula. These protrusions disappear at the completion of yolk absorption about five to ten days after hatching. *Oligocottus maculosus* larvae also possess a distinctive bubble of skin in the nape region just anterior to the origin of the dorsal finfold. This bubble persists in larvae up to 7.5 mm SL.

Flexion and postflexion larvae >6.5 mm possess a relatively low number of preopercular spines (9–13).

Postflexion larvae and juveniles may be distinguished by meristics, especially the high vertebral and dorsal fin ray counts, and the small size at transformation (8–9 mm SL). In addition, juveniles possess a slender postorbital cirrus and two frontoparietal cirri.

PIGMENTATION.—Newly hatched larvae of *O. maculosus* possess no melanistic head pigmentation. Fourteen to 16 intense, stellate melanophores are concentrated in the nape region. One to 3 dendritic melanophores extend anteriorly from the nape pigment patch onto a prominent elevation or bubble of skin located just anterior to the origin of the dorsal finfold. In live larvae, xanthophores cover the bubble of skin and the nape. Three to 4 dendritic, embedded melanophores are positioned in the otic capsule.

The dorsal surface of the gut is darkly pig-

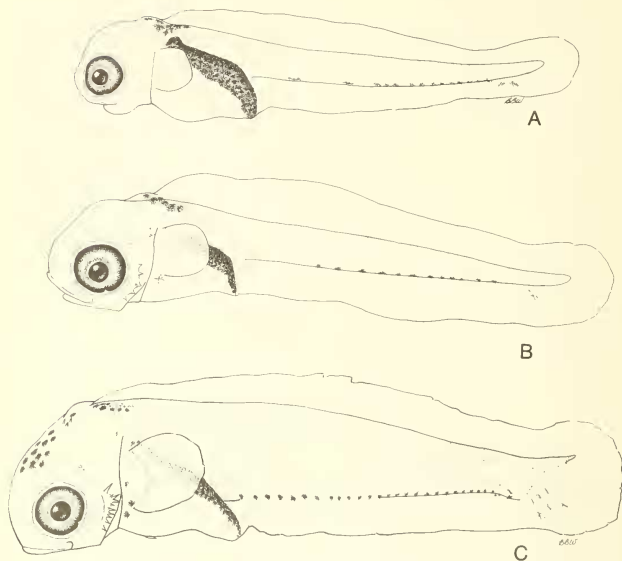


FIGURE 16. Larvae of *Oligocottus maculosus*: A) 4.3 mm NL, B) 7.2 mm NL, C) 6.9 mm NL.

mented with 100–150 dark melanophores. Two to 4 pale, dendritic melanophores are located along the anteroventral margin of the gut, just beneath the pectoral fins. These melanophores are frequently embedded in the gut musculature and are difficult to see. One to 5 small melanophores are clustered around the anus.

Posterior to the anus, larvae of *O. maculosus* possess a relatively high number of ventral midline melanophores. The actual number of melanophores appears to vary with the geographic location at which the larvae were collected. Stein (1973) recorded between 11 and 20 ventral midline melanophores in his reared larvae, while larvae reared in Oregon possessed between 16 and 20 melanophores along the ventral midline. J. B. Marliave (Vancouver Public Aquarium, Van-

couver, B.C., Canada, pers. comm.) found between 26 and 36 ventral midline melanophores in reared larvae from the Straits of Georgia in British Columbia. Regardless of the number of melanophores, this series begins under the third or fourth myomere posterior to the anus and extends toward the tail tip. The first four melanophores in the series are usually spaced one every two to three myomeres, while the remainder of the melanophores are spaced one per myomere. Five or nine additional pigment slashes extend onto the ventral finfold near the tail tip.

During larval development in larvae <6 mm, 15–20 melanophores form over the midbrain and interorbital region of the head. Two to 5 melanophores form on the snout and 1–3 melanophores form on the cheek just anterior to the

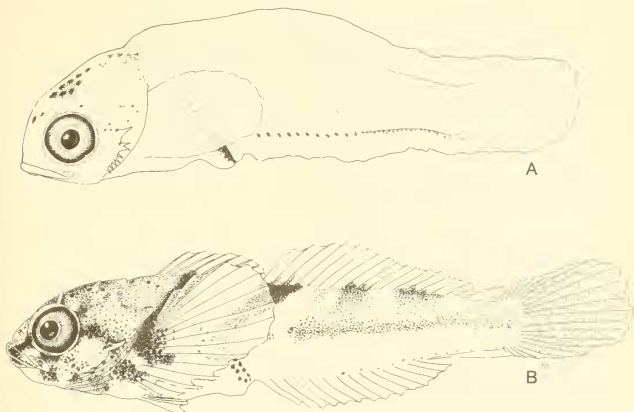


FIGURE 17. Young of *Oligocottus maculosus*: A) 7.8 mm SL, B) 10.4 mm SL.

dorsalmost preopercular spine in larvae >7 mm. At this size, melanophores are also added in the otic capsule; however, they become obscured by the developing musculature and are difficult to see. By ~ 6 mm, several melanophores are added just ventral to the nape pigment patch. Five to 7 of the centrally positioned melanophores become embedded while the other nape melanophores form a prominent U-shape anterolaterally around the central melanophores.

During transformation, ~ 7 –8 mm, melanistic pigmentation increases markedly over the dorsal surface of the head. Melanophores are added on the snout, on the cheek region anterior to the preopercle and on the dorsal portion of the operculum. Melanophores also form on the pectoral fin base and gradually extend ventrally onto the isthmus.

Pigmentation over the dorsal surface of the head is intense in benthic juveniles. A band of melanophores forms on either side of the snout, extending from the upper lip to the ventral margin of each eye. Each band continues posteriorly reaching from the eye to the dorsalmost preopercular spine. Melanophores are also added ventrally along the entire margin of the pre-

operculum and on the anterior tip of the lower lip. In juveniles >8.5 mm, tiny melanophores cover the entire dorsolateral surface of the head; however, the bands of pigment extending through each eye remain prominent. An irregular band of tiny melanophores forms along the surface of the lateral midline in juveniles ≥ 9 mm. This band gradually extends posteriorly to the caudal fin base. Two additional bands of pigment form along the dorsum. A third band forms under the 8th–10th dorsal rays and a fourth band develops under the 14th–16th dorsal fin rays. These pigment bands eventually extend ventrally and fuse with the lateral midline pigmentation. Tiny melanophores are added over the dorsolateral body surface in juveniles ~ 13 mm; however, the intense pigment bands along the dorsum remain distinct. Melanophores extend out onto the dorsal and caudal fin rays, forming three or five bands of pigment.

MORPHOLOGY.—Newly hatched *Oligocottus maculosus* larvae range in length from 4.2 to 4.5 mm NL. Larvae undergo flexion of the notochord at 7.2–7.6 mm NL. Transformation occurs at a relatively small size, ~ 7.5 –8 mm. The smallest benthic juvenile examined was 8 mm long.

TABLE 5. BODY PROPORTIONS OF LARVAE AND JUVENILES OF *OLIGOCOTTUS MACULOSUS* AND *O. SNYDERI*. Values are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses.

Item	<i>Oligocottus maculosus</i>	<i>Oligocottus snyderi</i>
Head length/SL:		
Preflexion	17.3 ± 0.61 (17.2-18.3)	21.4 ± 1.26 (20.1-23.4)
Flexion	19.7 ± 1.84 (18.4-21.0)	20.8 ± 1.34 (18.9-23.1)
Postflexion	25.3 ± 1.89 (22.3-26.6)	23.4 ± 1.71 (21.4-28.2)
Juvenile	30.1 ± 3.06 (27.1-32.8)	26.9 ± 1.00 (26.5-28.0)
Snout length/HL:		
Preflexion	25.7 ± 2.08 (24.3-27.9)	23.7 ± 3.37 (21.2-25.9)
Flexion	26.5 ± 1.08 (26.0-28.1)	21.4 ± 2.43 (16.9-23.3)
Postflexion	29.3 ± 2.83 (24.4-33.0)	16.1 ± 2.87 (13.9-20.4)
Juvenile	27.1 ± 3.22 (24.9-31.4)	32.0 ± 0.00 (32.0-32.0)
Eye diameter/HL:		
Preflexion	55.6 ± 2.08 (53.9-57.2)	47.8 ± 4.80 (40.1-52.3)
Flexion	44.9 ± 4.24 (42.3-48.2)	42.1 ± 2.95 (37.6-46.1)
Postflexion	41.2 ± 4.03 (33.1-45.0)	33.3 ± 3.21 (31.2-37.9)
Juvenile	31.4 ± 2.01 (28.9-34.1)	31.0 ± 2.52 (29.0-34.3)
Snout to anus length/SL:		
Preflexion	39.1 ± 1.53 (37.2-40.4)	42.1 ± 1.47 (40.1-44.4)
Flexion	39.8 ± 2.83 (38.1-42.3)	41.8 ± 2.30 (39.2-44.9)
Postflexion	43.9 ± 3.39 (40.8-48.1)	44.5 ± 1.83 (42.1-46.4)
Juvenile	45.0 ± 2.65 (42.7-48.5)	42.2 ± 1.53 (40.3-43.1)
Snout to pelvic fin origin/SL:		
Preflexion	-	-
Flexion	24.0*	21.0 ± 1.00 (20.0-22.0)
Postflexion	24.9 ± 2.15 (23.1-26.9)	23.3 ± 1.71 (21.0-25.5)
Juvenile	28.1 ± 3.61 (25.3-32.1)	24.6 ± 1.53 (22.9-26.1)
Pelvic fin origin to anus/SL:		
Preflexion	-	-
Flexion	18.0*	20.0 ± 1.15 (19.1-21.1)
Postflexion	20.2 ± 1.89 (18.1-22.8)	21.2 ± 1.50 (20.1-23.3)
Juvenile	16.9 ± 1.73 (16.1-19.4)	18.1 ± 3.21 (16.0-22.1)
Body depth at pectoral fin base/SL:		
Preflexion	19.4 ± 1.00 (17.8-20.2)	23.2 ± 1.17 (21.8-25.5)
Flexion	24.0 ± 0.00 (24.0-24.0)	23.4 ± 2.00 (20.2-26.6)
Postflexion	25.9 ± 2.17 (23.7-29.1)	20.6 ± 1.50 (19.4-21.8)
Juvenile	23.9 ± 3.06 (20.6-27.2)	21.2 ± 2.00 (19.0-23.4)
Body depth at anus/SL:		
Preflexion	15.5 ± 0.61 (14.9-16.2)	21.0 ± 2.37 (18.1-24.9)
Flexion	18.0 ± 0.00 (18.0-18.0)	24.3 ± 2.91 (17.9-28.1)
Postflexion	25.9 ± 2.17 (23.7-29.1)	26.2 ± 1.50 (21.9-27.3)
Juvenile	20.3 ± 2.08 (18.1-22.3)	22.1 ± 2.31 (19.0-23.0)
Pectoral fin length/SL:		
Preflexion	10.1 ± 0.61 (9.8-11.2)	8.2 ± 2.53 (6.1-12.1)
Flexion	18.0 ± 0.00 (18.0-18.0)	10.1 ± 1.77 (9.3-13.4)
Postflexion	21.7 ± 2.96 (17.3-26.3)	14.4 ± 1.41 (13.1-16.0)
Juvenile	29.1 ± 2.65 (26.8-31.9)	24.3 ± 1.53 (22.9-26.3)

- - Not present at this stage.

* = Only one specimen available in this stage.

Eighteen specimens of *O. maculosus* (4.3-10.8 mm) were examined for developmental morphology.

In newly hatched larvae two prominent bumps

or protrusions appear on the dorsal surface of the gut just posterior to the pectoral fin base. These bulges are similar to the dorsal gut diverticula of *Artemis* larvae; however, they never

develop into distinct diverticula. The gut protrusions disappear approximately 5–10 days after hatching. *Oligocottus maculosus* larvae also possess a distinctive bubble of skin in the nape region just anterior to the origin of the dorsal finfold. This bubble persists in larvae ≤ 7.5 mm.

Small *O. maculosus* are slender with a relatively short gut. Snout to anus length averages 39% in preflexion larvae and increases to 44% in postflexion larvae and 45% SL in juveniles. Body depth at both the pectoral fin base and the anus increases during larval development from 19% and 15%, respectively, to 25% SL.

FIN DEVELOPMENT.—Larval *Oligocottus maculosus* begin to undergo notochord flexion at ~6–7 mm. The adult complement of 12 principal caudal rays is complete in larvae ~6.8–7 mm long at about the completion of notochord flexion.

Dorsal and anal fin rays begin to form in larvae ~6.6 mm long; however, the full complement of fin rays (15–18, 12–14, respectively) is not complete until larvae are 8 mm long. Dorsal spines (VIII–IX) also form between 7 and 8 mm. Although pectoral fin rays are visible in larvae by 6.6 mm, the adult complement (12–15) is not fully formed until larvae reach about 7.6 mm. Pelvic buds are first visible in 7 mm larvae but the fin rays are not formed until ~8.5 mm.

SPINATION.—Six to 7 tiny spines are first visible on the posterior margin of the preopercle in larvae ~5.8 mm long. Spines increase in number to 9 or 10 in larvae undergoing notochord flexion. In postflexion larvae 6.9–7.8 mm long, preopercular spines number 10 or 11. Two or 3 of these spines appear as tiny accessory spines that form just anterior to the bases of the other spines. The dorsalmost spine becomes slightly larger than the lower spines. The 3rd, 4th, and 5th preopercular spines also increase slightly in size relative to the lower spines. In the largest planktonic larvae (~8 mm long) the preopercular spines begin to decrease in size and number and are covered with skin. In newly settled benthic juveniles ~8–10 mm long, the dorsalmost spine is quite large and stout with a strong upward curvature. The lower spines persist only as three blunt, bony protrusions on the preopercular margin.

Three tiny spines also form in the parietal region in larvae ~6–7 mm long. Two spines develop anteriorly with a third nuchal spine forming just posterior to them. These parietal spines persist through the larval period, but they regress

in benthic juveniles. During regression, the anterior spines decrease in size and their tips bend posteriorly and fuse with the nuchal spine, forming an arch. This canal and arch become incorporated into the cephalic lateral line system.

Two spines also form on the posttemporal in larvae ~6–7 mm long. By ~7–8 mm, a third spine forms on the posttemporal and a fourth spine forms on the supracleithrum. These supracleithral-posttemporal spines persist through larval development and eventually form the junction of the cephalic and lateral line systems.

Oligocottus snyderi

(Figures 18, 19; Table 5)

LITERATURE.—Stein (1973) described and illustrated 4.5- and 5.5-mm TL larvae of *O. snyderi*. Richardson and Washington (1980) called these larvae Cottidae Type 1 and illustrated specimens 4.2, 6.7, and 9 mm long.

IDENTIFICATION.—Small larvae in this series were reared from eggs spawned from known adults. Adults and juveniles were identified by the following combination of characters: high vertebral (34–37) and dorsal fin ray (17–20) counts, light pigmentation, the presence of cirri on the nasal spines and along the bases of the dorsal fins, and the absence of scales (prickles). The developmental series was linked together primarily on the basis of pigmentation, body shape, and preopercular and parietal spination. Postflexion and transforming larvae were linked to juveniles by pigmentation, meristics, and preopercular and parietal spination.

DISTINGUISHING FEATURES.—Distinguishing pigmentation of preflexion larval *O. snyderi* are melanistic nape pigmentation, relatively light pigmentation over the dorsolateral surfaces of the gut, and a low number of ventral midline melanophores (5–9) situated posterior to the anus. This series of ventral midline melanophores originates beneath the fifth to seventh postanal myomeres and extends posteriorly toward the tail tip. One melanophore is spaced approximately every four or five myomeres. This characteristic pigmentation changes little during larval development.

In newly hatched larvae, a hump or bubble of skin is present just anterior to the origin of the dorsal finfold. Although diffuse xanthophores are present over this bump in laboratory-reared larvae, no melanophores extend onto this bubble of skin. In contrast, *O. maculosus* larvae, which

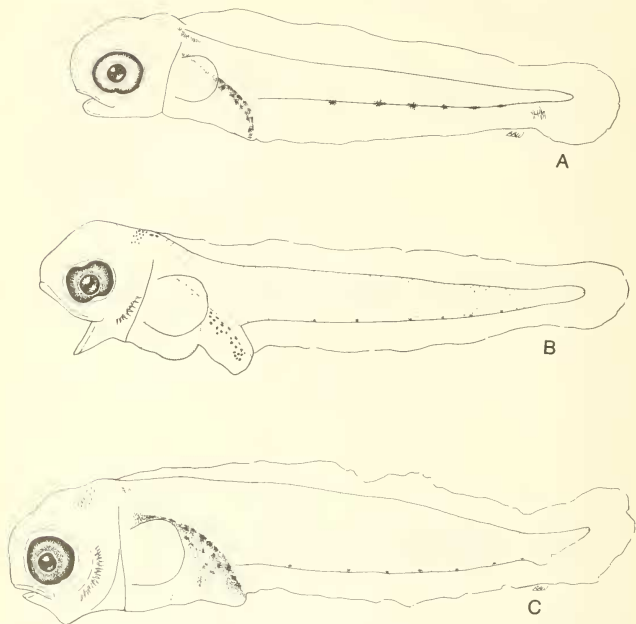


FIGURE 18. Larvae of *Oligocottus snyderi*: A) 4.7 mm NL, B) 5.1 mm NL, C) 6.7 mm NL (C from Richardson and Washington 1980).

also possess this distinctive bubble of skin at the nape, have one to three large dendritic melanophores that extend up onto the bubble of skin from the nape pigment patch.

Larvae of *O. snyderi* >4.2 mm NL may be further distinguished from all other known cottid larvae by the presence of a cluster of 10–20 minute prickles situated in the parietal region of the head.

Larvae undergoing notochord flexion, >6 mm long, possess a distinctive pattern of multiple preopercular spination, in which approximately 15 equal-sized spines are positioned along the

posterior margin of the preopercle. Ten to 11 small, accessory spines are situated at the anterior bases of the other spines and point anterolaterally.

Postflexion larvae and juveniles may be distinguished by their relatively light pigmentation, the prominent bands of pigment through the eye, and the low number of widely spaced ventral midline melanophores. In addition to pigmentation, juvenile *O. snyderi* are characterized by high vertebral and dorsal fin ray counts (34–37 and 17–20, respectively), and by the presence of very long, slender nasal, postorbital, and fron-

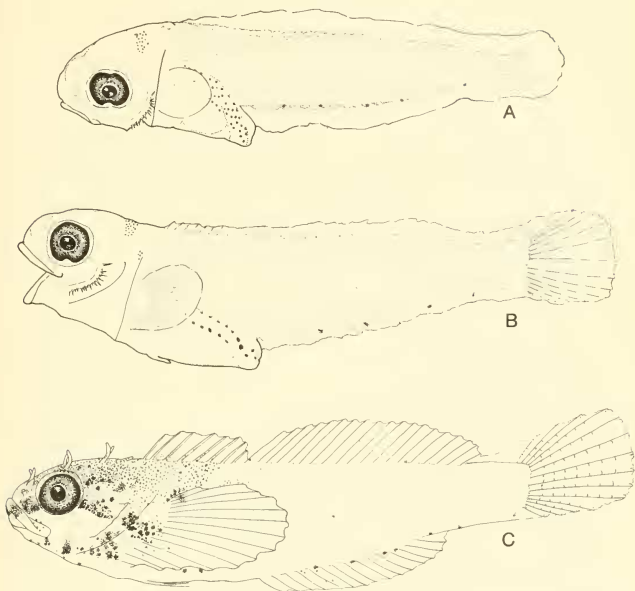


FIGURE 19. Young of *Oligocottus snyderi*: A) 8.2 mm SL, B) 10.2 mm SL, C) 14.4 mm SL.

toparietal cirri. In juveniles >15 mm, a row of distinctive cirri develop along either side of the bases of the dorsal fins.

PIGMENTATION.—Newly hatched, reared larval *O. snyderi* are lightly pigmented with no melanistic head pigmentation. Several xanthophores are situated over the midbrain in live larvae. Two to 8 external melanophores are clustered over the notochord in the nape region. In live specimens several diffuse xanthophores extend dorsally from the nape onto a distinctive bump or bubble of skin just anterior to the origin of the dorsal finfold. In contrast to larvae of *O. maculosus*, however, melanophores never extend onto this bubble of skin in larvae of *O.*

snyderi. The dorsolateral surface of the gut is lightly pigmented with 50–60 small melanophores forming an elliptical patch over the body cavity. Intense xanthophores also cover the dorsolateral surfaces of the gut. The only pigmentation posterior to the anus consists of a series of 5–9 melanophores that originates under the fifth to seventh postanal myomere and extends posteriorly. Each melanophore is positioned four to six myomeres apart. Occasionally, one or two melanistic pigment slashes extend onto the caudal finfold just beneath the notochord tip.

During larval development, several melanophores form on the dorsal surface of the head. Size of larvae at formation of this melanistic pig-

mentation appears somewhat variable. One or two melanophores are present over the midbrain in 21-day-old, laboratory-reared larvae (~6.5 mm long). Morris (n.d.) reported that four or five melanophores develop in the midbrain region of larvae at four weeks of age (~8.5 mm). Melanistic pigmentation does not appear over the brain in field-caught larvae until about 10 mm.

During transformation, head pigmentation increases markedly in late postflexion larvae 10–14 mm long. Thirteen to 18 large, stellate melanophores form over the midbrain and interorbital regions of the head. Concurrently, several small melanophores form anterior to the orbit and extend anteriorly across the snout onto the upper lip forming a distinct band. Several intense melanophores develop posterior to the orbit forming a dark band extending from the orbit to the dorsalmost preopercular spine. Melanophores are also added at the posterior margin of the lower jaw just ventral to the preopercle, along the dorsal margin of the operculum, and along the pectoral fin rays. A row of intense, embedded melanophores forms just above the spinal cord and extends posteriorly from the nape region two-thirds of the way to the caudal fin. The ventral midline melanophores remain unchanged.

In juveniles between 13 and 15 mm long, numerous tiny melanophores form over the dorsolateral surfaces of the head and extend anteriorly onto the snout between the eyes, ventrally along the preopercle, and along the opercular margin. These diffuse melanophores extend posteriorly to the seventh dorsal spine. Numerous small melanophores also form posterior to the pectoral fin base in an irregular band of pigment along the lateral midline. With development, melanophores are added along the dorsum in an anterior to posterior sequence. Concurrently, melanophores extend dorsally onto the dorsal fins forming four to five distinct bands of pigment. Gradually, the melanophores along the dorsal midline extend ventrally and posteriorly and join the dorsal and lateral areas of pigmentation. This lateral pigmentation extends posteriorly and forms a dark band at the base of the caudal fin. Melanophores extend onto the caudal fin rays forming four to five bands of pigment. Juvenile *O. snyderi* are characterized by uniform diffuse pigmentation over the head and dorsolateral surfaces of the body with a distinct, dark band of pigment extending from the snout, through the orbit, to the dorsalmost preopercular

spine. The characteristic low number of widely spaced ventral midline melanophores remains visible in juveniles ≤ 18 mm.

MORPHOLOGY.—Newly hatched *O. snyderi* larvae range in size from 4 to 4.5 mm NL. Notochord flexion occurs between 6.2 and 8.4 mm NL. The largest planktonic specimen taken in the field is 10.2 mm and has not yet begun to undergo transformation. The smallest benthic juvenile examined is 12.4 mm. Twenty-four specimens, ranging in length from 4 to 15.1 mm, were examined for development morphology.

Newly hatched *O. snyderi* larvae are rather slender with a relatively short gut, the posteriormost portion of which trails well below the body. Snout to anus length averages 42% in preflexion and flexion larvae, then increases slightly to 44% SL in postflexion larvae. Relative body depth at the pectoral fin base increases from 23% to 25% SL during larval development. A small, rounded protrusion extends dorsally from the dorsal surface of the gut just posterior to the pectoral fin base in newly hatched larvae. This protrusion is reminiscent of the gut diverticula found in larvae of several species of *Artedius* but is much less pronounced and never develops into distinct diverticula. This protrusion decreases in size shortly after hatching and is no longer visible by yolk absorption five days after hatching. In addition, *O. snyderi* larvae possess a prominent bump or bubble of skin that protrudes dorsally in the nape region just anterior to the origin of the dorsal finfold. This bubble persists in larvae up to ~6.5–7 mm.

FIN DEVELOPMENT.—Larvae of *O. snyderi* undergo notochord flexion between 6.2 and 8.4 mm. Caudal fin rays first appear at 7.8 mm; however, the full adult complement of 6 + 6 principal caudal rays is not complete until larvae reach ~9–10 mm. Rays begin to form in the dorsal and anal fins of larvae between 7.5 and 8 mm long; however, these rays are not fully formed in larvae <9 mm. Adult complements are 17–20 and 12–15, respectively. Dorsal fin spines begin forming in larvae 9–10 mm long, and the adult complement of spines (VIII–IX) is countable in a 10.2 mm specimen. Pectoral fin rays (12–15) form at 9 mm and are complete by 10 mm. Pelvic buds are first visible in larvae between 8.2 and 9 mm, but the fin rays are not fully formed until larvae reach 10–12 mm.

SPINATION.—Five to nine tiny bumps form along the posterior margin of the preopercle

in larvae >4.2 – 5 mm. By ~ 5.1 mm, 10–15 tiny equal-sized spines are visible. During notochord flexion the preopercular spines increase in size and number, ranging between 17 and 22. The preopercular spines of *O. snyderi* larvae are unique in that 10–12 spines form along the posterior margin of the preopercle as in other cottids with preopercular spines, yet by ~ 7 mm NL, between 8 and 10 small accessory spines form anteriorly at the bases of the original spines. In larvae >9 mm, the dorsalmost preopercular spine becomes stouter and longer than the other spines and is separated from the lower spines by a short gap on the preopercular margin. The 5–8 spines just ventral to the dorsalmost spine also become slightly larger relative to the lower preopercular spines. Between 12 and 14 preopercular spines are visible in newly settled benthic juveniles. The dorsalmost spine becomes much larger relative to the other spines. The smaller, accessory spines begin to atrophy and are represented only by small bumps or irregularities on the preopercle. By ~ 14 mm, only the dorsalmost spine persists.

Distinctive spines also form in the parietal region of the head of young *O. snyderi*. Larvae as small as 4.2 mm have 7–10 small bumps or prickles visible over the parietals. These prickles increase in number during development; 10–20 prickles are present in the parietal region in larvae ≥ 6.2 mm. Eight to 12 tiny prickles remain visible along the posterolateral margin of the parietal bones in 12–13-mm cleared and stained benthic juveniles.

A cluster of spines also develops in the supraclithral-posttemporal region in larvae >8 mm. One spine forms on the supraclithrum and five spines, situated in two rows, form on the dorsal portion of the posttemporal. These persist throughout larval development but atrophy during transformation until only three bony projections are present in benthic juveniles. These bony projections represent the rudiments of the incipient lateral line system.

Clinocottus acuticeps

(Figures 20–22; Table 6)

LITERATURE.—Blackburn (1973) illustrated and described an 8.6-mm specimen, which he called Cottid 1 “*Biramous anus*.” Richardson (1977) and Richardson and Percy (1977) listed larvae of *C. acuticeps* as Cottidae sp. 12. Larvae of this species were described by Richardson and Wash-

ington (1980). They illustrated specimens 3.7, 3.9, 6.9, 7.6, 10.4, 13.8, and 16.5 mm long.

IDENTIFICATION.—Small larval *C. acuticeps* were reared from eggs spawned from known adults. Adults and juveniles were identified by low dorsal fin ray (13–17) and anal fin ray (9–13) counts, the presence of nasal cirri, and a membrane connecting the innermost pelvic fin ray with the abdomen. The developmental series was linked together primarily by pigmentation, body shape, and hindgut diverticula. Postflexion and transforming larvae were linked with juveniles by pigmentation, meristics, and the membrane attaching the pelvic fin rays to the abdomen.

DISTINGUISHING FEATURES.—*Clinocottus acuticeps* larvae are distinguished from all other known cottid larvae by long protrusions (diverticula) that extend posteriorly from the gut on either side of the anus. These diverticula are present in yolk-sac larvae and persist in the largest pelagic specimens (14.5 mm). The gut itself is distinctively long and the posterior portion trails well below the body. Snout to anus length, averaging 62.5% SL, is greater than in other known larvae of *Artedius*, *Clinocottus*, or *Oligocottus*. In addition, these larvae have a flabby appearance with an outer bubble of skin, which is especially pronounced in the head region.

Other characters useful in distinguishing *C. acuticeps* larvae are melanistic pigmentation on the snout and head, and relatively few ventral midline melanophores (4–10).

Transforming and juvenile *C. acuticeps* are distinguishable from all other known cottids by the presence of a membrane attaching the inner pelvic fin ray to the belly. Other characters useful in separating juveniles are the relatively light, uniform pigmentation over the body; a band of pigment extending from the snout posteriorly through the orbit toward the preopercle; a dark blotch of pigment at the anterior end of the spinous dorsal; and a low number of ventral midline melanophores.

PIGMENTATION.—Newly hatched larvae reared in the laboratory exhibit 4 or 5 dendritic melanophores on the snout and 2 faint melanophores in each otic capsule. In field-collected larvae <3.7 mm NL, the presence of snout pigment varies; however, all larvae >3.7 mm NL possess at least 2 melanophores on the snout. Eight to 15 melanophores are clustered in the nape region of even the smallest larvae. Numerous melano-

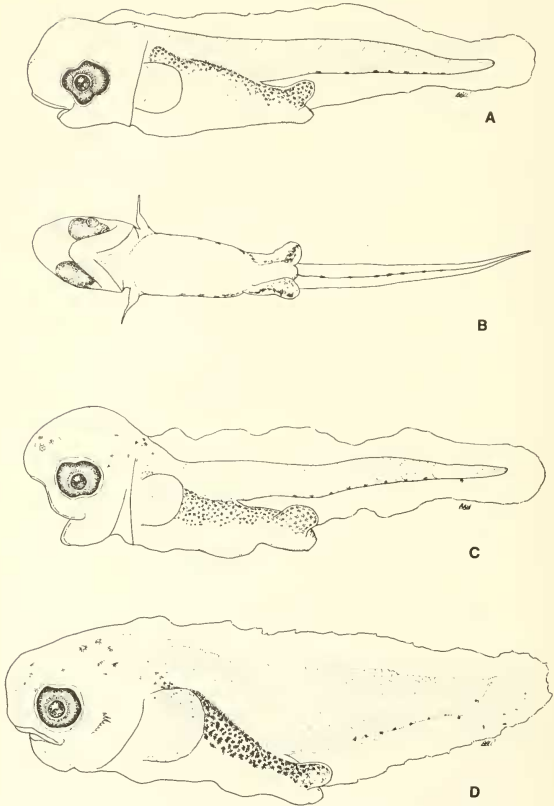


FIGURE 20. Larvae of *Clinocottus acuticeps*: A) 3.7 mm NL, B) 3.7 mm NL, C) 3.9 mm NL, D) 6.9 mm NL (from Richardson and Washington 1980).

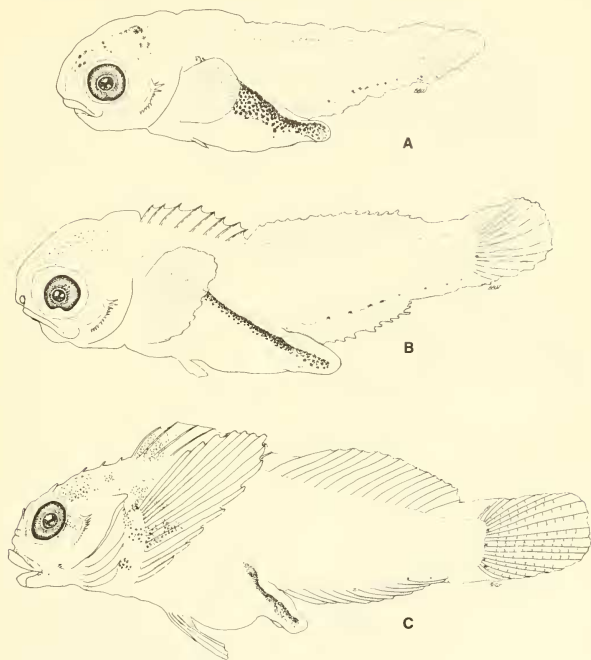


FIGURE 21. Larvae of *Clinocottus acuticeps*: A) 7.6 mm SL, B) 10.4 mm SL, C) 13.8 mm SL (from Richardson and Washington 1980).

phores are scattered over the dorsolateral surface of the gut extending posterolaterally over the surface of the gut diverticula. These melanophores are much fainter and more irregular in shape than in larvae of other species of *Clinocottus*.

A series of 4–10 inconspicuous ventral midline melanophores originates beneath the 7th–10th postanal myomeres and extends posteriorly toward the tail tip. Several additional melanophores appear as streaks of pigment on the ventral finfold near the tail tip.

Pigmentation increases on the head during larval development. Melanophores form first on the head over the midbrain in larvae 5.5 mm NL. Concurrently, several embedded melanophores appear on the nape and extend anteriorly onto the head. Four to five internal melanophores occur in or near the otic capsule. In larvae >6.5 mm, scattered melanophores extend continuously from the snout to the nape region. Ventral midline melanophores persist in flexion and postflexion larvae, and the posteriormost mel-

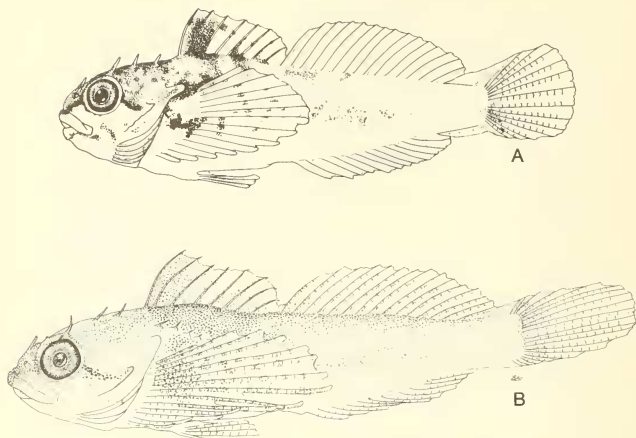


FIGURE 22. Young of *Clinocottus acuticeps*: A) 13.8 mm SL, B) 16.5 mm SL (B from Richardson and Washington 1980).

nophore, which is located near the notochord tip in small larvae, occurs near the middle of the caudal fin base between the forming hypural plates. The posteriormost melanophores which extended onto the ventral finfold now occur on the caudal fin. In the largest planktonic larvae, which are beginning to undergo transformation, melanophores are added in a patch just posterior to the orbit. Melanophores also are added along the bases of the pectoral fins and extend onto the pectoral fin rays.

In newly settled benthic juveniles (13–14 mm) head pigmentation increases markedly. Melanophores extend anteriorly across the dorsal surface of the snout and onto the upper lip. The melanophores at the ventral margin of the snout are especially intense and closely spaced, forming a prominent band that extends from the upper lip to the ventral margin of the orbit. This band continues from the posterior margin of the orbit to the dorsal margin of the preopercle. Additional melanophores are added along the ventral edge of the lower lip, at the base of the preopercle, and on the dorsal portion of the operculum. As development proceeds, a second band of pig-

ment forms between the ventral margin of the orbit and the melanophores at the base of the preopercle. Simultaneously, pigmentation increases on the pectoral fin bases while two to three bands of pigment form across each fin.

Between 14 and 15 mm, a dense patch of melanophores forms at the anterior end of the first dorsal fin between the first and third spines. As juvenile pigmentation progresses this patch expands posteriorly to include the fourth dorsal spine, and a second patch of melanophores forms between the seventh and eighth dorsal spines. Melanophores extend ventrally from these two pigment patches forming two distinct bands across the dorsum. Pigmentation proceeds posteriorly along the dorsum. In juveniles between 15 and 16 mm long, a third band (or saddle) of pigment forms under the second to sixth dorsal fin rays; a fourth band forms under the 8th to 11th dorsal fin rays; and a fifth band forms under the last two dorsal fin rays. As these bands of pigment develop along the dorsum, they extend ventrally and eventually unite into a uniform band of pigment above the lateral midline. Concurrently, another band of pigment extends pos-

TABLE 6. BODY PROPORTIONS OF LARVAE AND JUVENILES OF *CLINOCOTTUS ACUTICEPS*, *C. EMBRYUM*, *C. GLOBICEPS*, AND *C. ANALIS*. Values given are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses.

Item	<i>Clinocottus acuticeps</i>	<i>Clinocottus embryo</i>	<i>Clinocottus globiceps</i>	<i>Clinocottus analis</i>
Head length/SL:				
Preflexion	27.1 ± 3.44 (22.3–30.1)	26.1 ± 2.65 (26.0–30.1)	20.6 ± 2.21 (17.0–25.0)	–
Flexion	29.2 ± 1.92 (26.8–32.4)	23.9 ± 1.15 (21.8–25.3)	23.0 ± 1.79 (21.0–27.2)	–
Postflexion	27.9 ± 2.71 (22.9–32.6)	24.0 ± 0.00 (24.0–24.0)	27.3 ± 4.09 (22.4–33.3)	30.1 ± 1.25 (27.8–32.1)
Juvenile	32.2 ± 0.65 (31.5–32.7)	31.5 ± 1.13 (30.2–32.2)	31.6 ± 0.46 (31.2–32.1)	–
Snout length/HL:				
Preflexion	24.6 ± 4.80 (21.3–25.9)	21.3 ± 1.53 (19.9–23.7)	21.3 ± 4.40 (14.5–26.7)	–
Flexion	26.4 ± 2.97 (22.9–30.6)	24.1 ± 3.83 (18.4–30.8)	25.7 ± 3.39 (20.0–30.5)	–
Postflexion	23.6 ± 4.38 (16.3–30.9)	22.2 ± 0.58 (21.8–23.6)	25.3 ± 4.84 (20.0–33.0)	28.3 ± 2.70 (22.3–32.2)
Juvenile	27.5 ± 4.36 (26.8–29.4)	27.5 ± 1.47 (22.7–31.2)	27.1 ± 0.92 (26.1–27.9)	–
Eye diameter/HL:				
Preflexion	39.7 ± 6.63 (31.5–54.2)	39.3 ± 3.06 (35.8–42.1)	50.4 ± 9.16 (46.2–63.1)	–
Flexion	34.6 ± 2.41 (31.9–36.4)	35.7 ± 3.79 (34.8–39.5)	43.7 ± 7.39 (37.9–51.4)	–
Postflexion	32.7 ± 3.30 (27.1–38.2)	32.1 ± 3.06 (29.0–35.3)	38.2 ± 8.09 (24.4–46.0)	31.3 ± 1.41 (27.8–33.0)
Juvenile	27.9 ± 2.06 (25.5–29.3)	29.8 ± 0.74 (29.2–30.6)	27.1 ± 0.91 (26.1–27.9)	–
Snout to anus length/SL:				
Preflexion	60.7 ± 4.64 (54.4–67.2)	51.6 ± 3.51 (48.2–55.1)	44.0 ± 3.59 (39.6–52.9)	–
Flexion	62.8 ± 2.74 (60.3–67.1)	49.9 ± 3.87 (43.9–54.4)	48.2 ± 3.27 (44.4–56.0)	–
Postflexion	62.5 ± 4.61 (57.5–70.3)	50.0 ± 3.06 (47.3–53.8)	50.0 ± 3.48 (44.7–56.8)	48.9 ± 2.40 (46.4–54.3)
Juvenile	50.2 ± 1.64 (48.4–51.6)	49.0 ± 3.10 (47.0–52.6)	–	–
Snout to pelvic fin origin/SL:				
Preflexion	–	–	–	–
Flexion	–	28.0*	24.6 ± 2.94 (21.4–28.0)	–
Postflexion	33.4 ± 2.63 (29.4–39.5)	32.1 ± 3.54 (29.0–34.2)	26.7 ± 2.33 (23.4–30.9)	29.3 ± 1.34 (27.2–31.4)
Juvenile	33.3 ± 1.16 (32.5–34.6)	31.1 ± 1.31 (29.6–32.1)	30.7 ± 1.04 (29.5–31.4)	–
Pelvic fin origin to anus/SL:				
Preflexion	–	–	–	–
Flexion	–	26.1*	21.5 ± 1.77 (18.7–23.4)	–
Postflexion	29.4 ± 4.56 (23.1–37.3)	18.2 ± 0.71 (17.1–18.4)	22.9 ± 1.42 (21.4–25.2)	19.9 ± 2.26 (17.3–22.3)
Juvenile	16.9 ± 1.70 (15.9–18.9)	17.9 ± 2.50 (15.4–20.4)	20.7 ± 0.64 (20.0–21.2)	–
Body depth at pectoral fin base/SL:				
Preflexion	24.3 ± 3.25 (17.8–29.1)	25.8 ± 4.36 (21.2–29.4)	20.8 ± 2.87 (15.8–25.5)	–
Flexion	27.6 ± 2.30 (24.3–30.2)	26.3 ± 2.29 (23.7–30.2)	23.9 ± 2.02 (22.2–29.3)	–
Postflexion	31.3 ± 2.29 (28.4–35.0)	26.1 ± 1.53 (25.0–28.2)	26.8 ± 2.78 (22.1–30.9)	28.1 ± 1.36 (25.4–29.1)
Juvenile	26.1 ± 1.99 (23.9–27.8)	21.6 ± 1.01 (23.5–25.5)	27.3 ± 0.53 (26.7–27.7)	–
Body depth at anus/SL:				
Preflexion	21.4 ± 2.94 (18.0–24.5)	22.8 ± 4.36 (18.2–26.5)	17.5 ± 2.46 (13.6–21.6)	–
Flexion	25.4 ± 2.07 (23.3–28.1)	25.1 ± 1.51 (22.9–27.3)	21.2 ± 2.07 (17.7–24.0)	–
Postflexion	28.4 ± 2.43 (26.4–35.2)	27.0 ± 0.00 (27.0–27.0)	25.7 ± 3.04 (21.1–30.4)	25.7 ± 1.50 (25.0–29.1)
Juvenile	24.0 ± 2.28 (21.4–25.4)	23.3 ± 1.93 (22.1–25.5)	25.7 ± 2.08 (23.3–27.0)	–
Pectoral fin length/SL:				
Preflexion	11.4 ± 1.27 (9.6–13.3)	9.9 ± 3.46 (6.3–12.1)	12.1 ± 1.19 (9.6–13.8)	–
Flexion	11.0 ± 1.87 (9.9–14.5)	11.2 ± 2.75 (7.1–17.5)	12.3 ± 4.40 (7.5–22.0)	–
Postflexion	26.4 ± 5.95 (18.2–35.0)	32.0 ± 4.04 (30.1–37.0)	22.7 ± 6.00 (11.1–30.4)	29.3 ± 2.15 (24.8–32.3)
Juvenile	32.1 ± 1.74 (30.8–34.1)	33.4 ± 1.16 (32.1–34.2)	29.0 ± 0.82 (28.1–29.7)	–

– = Not present at this stage.

* = Only one specimen available in this stage.

teriorly along the lateral midline to the caudal fin where melanophores form a dark band at the base of the caudal fin. Melanophores extend onto the caudal fin rays where they form four or five bands across the fin. Clusters of melanophores extend first ventrally and then laterally from the lateral midline pigment band and gradually unite enclosing three to five small unpigmented circles below the lateral line. Three to six tiny melanophores remain visible along the ventral midline posterior to the anus in juveniles <17 mm long.

MORPHOLOGY.—*Clinocottus acuticeps* larvae hatch at the smallest length (3.1–3.3 mm NL) of any member of the genus. Notochord flexion occurs between 5.6 and 7.3 mm NL. The largest planktonic specimen collected is 14.5 mm and is beginning to undergo transformation. The smallest benthic juvenile examined is 12.6 mm. Thirty-seven selected specimens of *C. acuticeps*, ranging in length from 3.1–16.2 mm, were examined for developmental morphology.

Larvae of *C. acuticeps* have a distinctive, flabby appearance as if a loose bubble of outer skin surrounds the anterior part of the body.

Larvae are deep-bodied with a long, distinctive gut, the posterior portion of which trails well below the body. Snout to anus length remains relatively constant during larval development, averaging 63% SL. Prominent diverticula extend posteroventrally from the hindgut on either side of the anus. These diverticula are well developed throughout larval development but are not visible in benthic juveniles.

FIN DEVELOPMENT.—A 5.6 mm NL larva is just beginning notochord flexion and a concurrent thickening of the hypural region of the forming caudal fin. The adult complement of 6 + 6 principal caudal rays is present in a 6.8 mm specimen prior to completion of notochord flexion at ~7.5 mm. Bases of the dorsal and anal fin rays begin forming on a 6.9 mm larva. The full adult complement of dorsal (13–17) and anal (9–13) fin rays is present by ~8 mm. The adult complement of dorsal fin spines (VII–IX), however, is not present until ~8.7 mm.

Although pectoral fin rays are visible on a 6.9 mm larva, the full adult complement (13–15) is not complete until >7.6 mm. Pelvic fin buds appear just after completion of notochord flexion in a 7.6 mm larva; however, the fin rays are not fully formed until ~10 mm.

SPINATION.—Preopercular spines first appear as small bumps at 5.2 mm NL. Nine to 11 small spines are present by the onset of notochord flexion at ~6 mm. During flexion, spines remain small and evenly spaced with the 2nd and 3rd spines becoming slightly longer than the others. By completion of flexion, at 7.6 mm, 11–12 spines are present along the margin of the preopercle. The dorsalmost 3 spines are beginning to elongate and point dorsally. In a 10-mm cleared and stained specimen, the dorsalmost 3 spines are nearly four times as long as the ventral spines. In the largest planktonic larvae (13–14 mm long) the ventralmost spines are beginning to atrophy. The 3 dorsalmost spines are still prominent in a 15.2 mm juvenile, but the 8 ventral spines are minuscule, with their tips twisted and bent anteriorly. By ~19 mm, the lower spines have atrophied completely, and only the single large dorsalmost spine persists.

No spines develop in the parietal or supra-cleithral-posttemporal regions of the head in larvae or juveniles of this species.

Clinocottus embryum

(Figures 23–25; Table 6)

LITERATURE.—Richardson (1977) and Richardson and Percy (1977) listed larvae of this species as Cottidae sp. 20. Richardson and Washington (1980) described these larvae as Cottidae Type 2 and illustrated specimens 4.0, 6.4, and 7.4 mm long.

IDENTIFICATION.—Juveniles and adults were identified using a combination of the following characters: an advanced anus, light pigmentation, presence of a nasal cirrus, low anal fin ray counts (9–12), and absence of a membrane attaching the pelvic fin rays to the abdomen. The developmental series was linked together primarily on the basis of pigmentation, body shape, and preopercular spination. Postflexion and transforming larvae were linked to juveniles by pigmentation, cirri patterns, meristics, and preopercular spination.

DISTINGUISHING FEATURES.—Characters useful in distinguishing preflexion larvae of *C. embryum* are lack of head pigment, relatively light gut pigmentation, large number of ventral midline melanophores (15–21), and relatively long, trailing gut. Head and/or snout pigment is present in larvae of all other species of *Clinocottus*. *C. embryum* larvae are further distinguished from

yolk-sac *C. acuticeps* larvae (in which snout pigment is sometimes absent) by the absence of distinct hindgut diverticula.

In addition to the pigmentation characters mentioned above, flexion and postflexion larvae of *C. embryum* are distinguished by their head spination. Larvae 7.3 mm have 11–14 preopercular spines; the dorsalmost spine is the largest.

In benthic juveniles of *C. embryum*, the anus is advanced midway between the origin of the pelvic fins and the anal fin, as in other members of the genus. Juvenile *C. embryum* are distinguished from *C. globiceps*, *C. analis*, and *C. recalvus* by relatively light, mottled body pigmentation and long and slender nasal, postorbital, and frontoparietal cirri. *Clinocottus embryum* juveniles are distinguished from *C. acuticeps* by the presence of a large number of ventral midline melanophores (15–21) and the absence of a membrane connecting the inner pelvic fin ray to the abdomen.

PIGMENTATION.—Melanistic pigmentation is absent on the head in preflexion *C. embryum* larvae. One to 5 melanophores are scattered over the nape region. The dorsolateral surface of the gut is relatively lightly pigmented and occasionally several faint melanophores are present on the anterolateral surface of the gut below the pectoral fins. Posterior to the anus, a series of 15–19 melanophores extends along the ventral midline. This series begins on the fourth or fifth myomere posterior to a vertical line through the anus; the melanophores are spaced approximately 1 per myomere. Several specimens have 1 or 2 melanophores on the ventral finfold near the notochord tip.

During larval development, the formation of head pigmentation varies in larvae between 6 and 9 mm long. Three out of eight larvae observed possess one to five tiny melanophores over the brain. One or two melanophores are consistently present beneath the pectoral fin on the anterolateral surface of the gut in larvae >6.5 mm. Otherwise, pigmentation remains unchanged.

In transforming larvae >9.6 mm long, numerous melanophores appear over the brain. Several melanophores appear on the cheek region between the orbit and the preopercle. Melanophores are also added on the pectoral fin base.

Melanistic pigmentation increases over the

head in newly settled juveniles. Large melanophores cover the surfaces of the head over the midbrain and interorbital regions. Several large, intense melanophores are embedded at the posterior margin of the parietal region. A distinct, dense band of melanophores extends from the orbit anteriorly onto the upper lip and posteriorly from the orbit to the dorsal tip of the preopercle. Several melanophores form a dark patch on the cheek beneath the orbit. Melanophores are also added to the dorsal surface of the operculum and to the pectoral fin base with several melanophores extending onto the pectoral fin rays.

As development proceeds, pigmentation increases markedly over the head. In a 16-mm juvenile, the bands of pigment extending through the eye are prominent, but numerous small melanophores cover the entire dorsal surface of the head above these bands of pigment. Pigmentation increases on the operculum and pectoral fin base. Three to four bands of melanophores are added across the pectoral fin rays.

Five bands of pigment develop on the body along the dorsal midline in an anterior to posterior sequence. The first band of pigment forms under the third to fifth dorsal fin spines, and a second smaller band begins to form under the seventh to ninth dorsal spines in juveniles between 13 and 14 mm long. By ~15 mm, three additional bands of pigment are present on the dorsum beneath the second dorsal fin. The third band forms under the 2nd–4th dorsal fin rays, the fourth band forms under the 7th–9th fin rays, and the fifth band forms under the 12th–15th rays. At the same time, a series of embedded melanophores develops in a row just above the notochord, extending from the nape region toward the caudal fin. A few diffuse patches of external melanophores also form along the lateral midline posterior to the gut.

As juvenile pigmentation develops, the dorsal bands of pigment extend ventrally until they unite above the lateral line, forming four unpigmented saddles between the bands. The melanophores lying along the lateral midline increase in number and extend posteriorly and ventrally toward the caudal fin. As this lateral pigmentation extends posteriorly, it fuses dorsally with the pigment bands. As pigmentation expands and unites over the lateral surface of the body, numerous, irregular, unpigmented circles remain above and below the lateral line, giving juvenile *C. embryum*

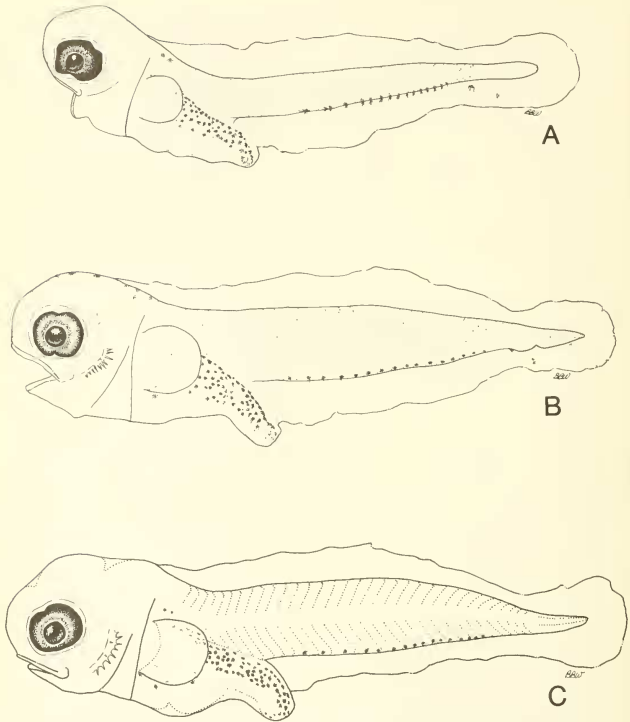


FIGURE 23. Larvae of *Clinocottus embryum*: A) 4.0 mm NL, B) 5.4 mm NL, C) 6.4 mm NL (A and B from Richardson and Washington 1980).

a distinctively mottled appearance. Eighteen to 21 small melanophores remain visible along the ventral midline in juveniles up to ~19 mm long.

MORPHOLOGY.—The smallest *C. embryum* examined is 4.0 mm NL and is recently hatched. Larvae undergo flexion of the notochord between 6.4 and 9.6 mm NL. The largest specimen taken

in the plankton is 14.0 mm and is beginning to undergo transformation. The smallest benthic juvenile is 13.7 mm. Eighteen *C. embryum*, ranging from 4 to 14 mm long, were examined for developmental morphology.

Larval *C. embryum* have a distinctively shaped gut with the posterior portion trailing well below

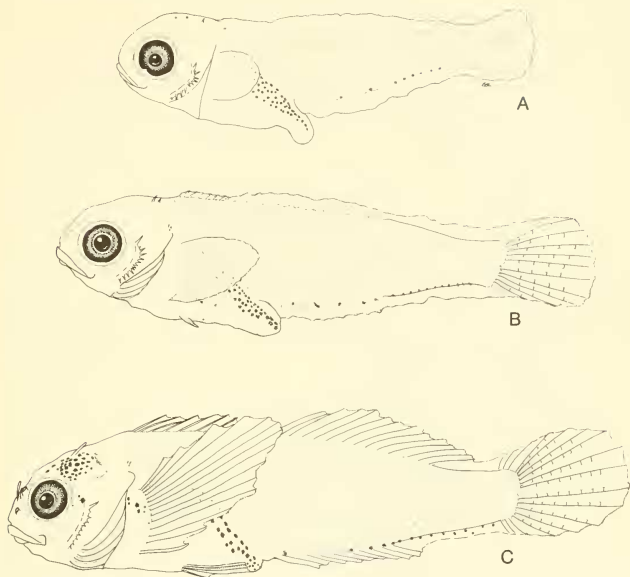


FIGURE 24. Larvae of *Clinocottus embryum*: A) 7.4 mm SL, B) 9.6 mm SL, C) 13.9 mm SL (A from Richardson and Washington 1980).

the body. The walls of the hindgut protrude on either side of the anus, reminiscent of the hindgut diverticula of *C. acuticeps*; however, these bulges never develop into pronounced diverticula. Snout to anus length is relatively long throughout larval development, averaging 50% SL.

FIN DEVELOPMENT.—The onset of notochord flexion is first apparent in a 6.4 mm larva. Caudal rays are present by ~7.4 mm but the adult complement of 6 + 6 principal caudal rays is not complete until about 8.4 mm. Bases of the forming dorsal and anal fin rays are first visible at ~7.4 mm; however, the adult complement of dorsal (14–17) and anal (9–12) fin rays is not present until ~8.3 mm. Dorsal spines (VIII–X)

are beginning to form at ~8.3 mm but are not fully formed until 9.6 mm. Pectoral fin rays begin to form at ~8 mm, and the adult complement of fin rays (12–15) is present by 9.6 mm. Pelvic fin buds are first apparent at ~9.6 mm, and the adult pelvic fin complement (1,3) is present in postflexion larvae >12.4 mm long.

SPINATION.—Eight to 10 tiny, evenly spaced spines increases, ranging in number from 11 to 14, opercle at ~5.2 mm NL. In larvae undergoing notochord flexion, the number of preopercular spines increases, ranging in number from 11 to 14. During the flexion stage, the dorsalmost preopercular spine increases in size relative to the rest of the preopercular spines so that by the end

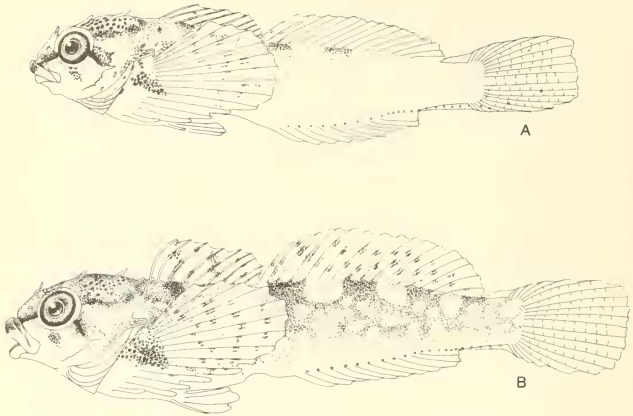


FIGURE 25. Juveniles of *Clinocottus embryum*: A) 13.7 mm SL, B) 16.2 mm SL.

of flexion. the dorsalmost spine is much longer and stouter than the other spines. In the largest planktonic larvae, 13–14 mm long, the upper spine is ≥ 2.5 times longer than the other spines and is separated from them by a slight gap. In newly settled benthic juveniles, the number and size of the lower preopercular spines are reduced. By > 15 mm, only a second, tiny spine persists just ventral to the large dorsal spine. The other spines appear as five to seven small bumps or irregularities along the preopercular margin. In completely transformed juveniles ≥ 16 mm long, only the uppermost spine is visible.

Two spines develop in the parietal region of *C. embryum* larvae. A single small spine is first present at the posterior margin of each parietal at ~ 6.7 mm. By 9.6 mm, this parietal spine has increased in size and a second smaller parietal spine is present just behind it. As larvae undergo transformation, between 12 and 14 mm, these spines undergo a reduction in size, and the first parietal spine eventually fuses with the second parietal spine, forming a hollow central canal between the spines. This canal is part of the incipient cephalic lateral line system. In newly set-

tled juveniles, only a skin-covered bony protuberance is visible in the parietal region.

Three spines also form in the supracleithral-posttemporal region of the head at ~ 9.6 mm. These spines persist through transformation and eventually become associated with the lateral line system in juveniles > 15 mm long.

Clinocottus globiceps

(Figures 26–28; Table 6)

LITERATURE.—Larvae of this species were listed by Richardson (1977) and Richardson and Pearcy (1977) as *Oligocottus* sp. 1. Richardson and Washington (1980) described larvae of this species as Cottidae Type 3. They illustrated specimens 6.3, 7.5, and 12.5 mm long.

IDENTIFICATION.—Larvae were reared from eggs spawned from known adults. Field-collected larvae were identified through comparison with reared larvae. Identification of larvae and juveniles was further confirmed by the following characters: pigmentation, body shape, an advanced anus, and absence of a nasal cirrus.

DISTINGUISHING FEATURES.—Preflexion and flexion larvae of *C. globiceps* may be distin-

guished from other cottid larvae, except *C. recalvus* and *C. analis*, by the presence of heavy pigmentation on the head, nape, and dorsolateral surface of the gut. Larval *C. globiceps* are distinguished from *C. recalvus* and *C. analis* by the number (4–8) and spacing of ventral midline melanophores. Late flexion and postflexion larvae of *C. globiceps* differ from all other *Clinocottus* larvae in preopercular and parietal spination.

Transforming and juvenile *C. globiceps* are distinguished from other cottid larvae by the combination of a blunt, rounded snout and head, heavy pigmentation over the anterior third of the body, and two or three inconspicuous ventral midline melanophores which persist on the caudal peduncle.

PIGMENTATION.—Newly hatched and preflexion larvae of *C. globiceps* have intense melanistic pigmentation on the head and nape. Eight to 11 large stellate melanophores are present over the midbrain and 21–30 melanophores are concentrated in the nape region. These nape melanophores are arranged in a distinctive pattern in which 7–10 melanophores are embedded along the dorsal midline of the nape and are surrounded anteriorly and laterally by 14–23 dark melanophores lying on the external surface of the nape. Eight to 10 dendritic melanophores occur on both the anterior and posterior walls of the otic capsules. The dorsolateral surface of the gut is heavily pigmented with 100–150 large, round melanophores. The only pigmentation occurring posterior to the anus is a series of 4–8 discrete, ventral midline melanophores. These are situated under the 10 posteriormost myomeres near the tail tip. Frequently, 2–5 additional small melanophores extend beyond the tail tip onto the caudal finfold.

Pigmentation changes little during larval development. The midbrain melanophores increase in number ranging from 12 to 16 in larvae >6 mm. By about 8 mm, melanophores are densely concentrated over the nape and extend anteriorly onto the head. Melanophores are added in the midbrain region and several melanophores extend anteriorly over the forebrain onto the snout. As head musculature develops, melanophores in the otic region become obscured so that only 5 or 6 melanophores are visible on the posterior wall of the otic capsule.

During transformation, in planktonic larvae 12–14 mm long, head pigmentation increases

markedly. Several melanophores are added on the upper lip and beneath the orbit. Melanophores are also added in a row along the preopercle and on the dorsal portion of the operculum. Pigmentation over the brain intensifies and expands posteriorly, merging with the nape pigmentation. Concurrently, nape melanophores extend ventrally from the nape forming a continuous band of pigment between the nape and gut. Pigmentation also increases over the body cavity as melanophores extend ventrally over the lateral surfaces of the gut. Several melanophores also are added on the pectoral fin base. Ventral midline melanophores decrease in size and number, until only two to four inconspicuous melanophores persist beneath the caudal peduncle.

Newly settled benthic juveniles of *C. globiceps* are distinctively pigmented with the anterior third of the body covered with dark melanophores extending posteriorly to about a vertical through the seventh dorsal spine. Only the posterior two-thirds of the pelvic fin rays remain unpigmented. Posterior to the intense head pigment, the two to four small, ventral midline melanophores constitute the only pigment. Between 14 and 16 mm SL, juvenile pigmentation is added posteriorly along the dorsum. By about 14 mm, a dark vertical bar of melanophores forms under the second to fourth dorsal fin rays and extends ventrally two-thirds of the way below the lateral midline. Between 15 and 16 mm, three additional saddles of melanophores are added posteriorly along the dorsum. The first saddle forms under the 8th–10th dorsal fin rays, the second forms under the 14th–15th fin rays, and the third saddle forms on the dorsal surface of the caudal peduncle. Concurrently, melanophores are added posteriorly along the lateral midline forming a dark band of pigment at the base of the caudal fin. Several melanophores appear on the pectoral, dorsal, and caudal fin rays.

MORPHOLOGY.—Larval *C. globiceps* hatch at a relatively large size, 5.1–5.4 mm NL. Flexion of the notochord occurs between 6.2 and 8.1 mm NL. The largest planktonic larva taken in field collection is 12.9 mm and is beginning to undergo transformation. The smallest benthic juvenile is 13.5 mm long. Thirty-eight specimens (5.1–14.6 mm) were examined for developmental morphometrics. Because only 10 larvae were available from field collections, this morphometric series includes 25 laboratory-reared larvae.

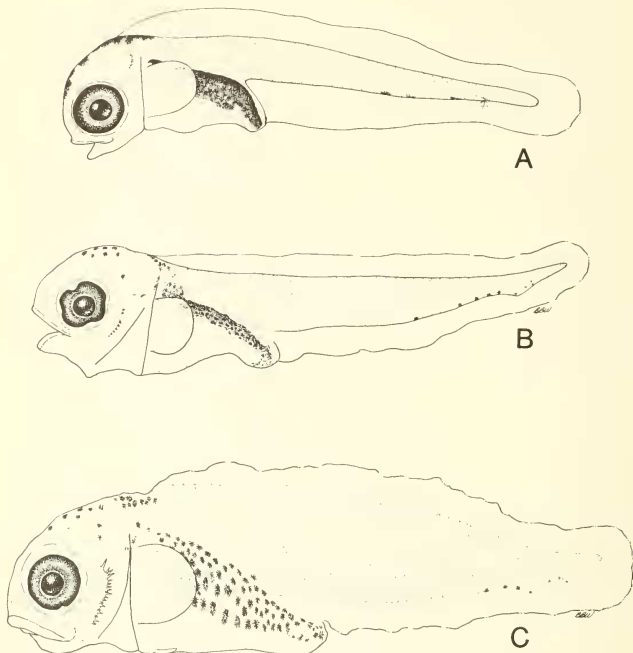


FIGURE 26. Larvae of *Clinocottus globiceps*: A) 5.0 mm NL, B) 6.3 mm SL, C) 7.5 mm NL (B and C from Richardson and Washington 1980).

Larval *C. globiceps* are relatively deep-bodied, and the posterior portion of the gut trails below the rest of the body. When viewed ventrally, the hindgut bulges slightly on either side of the anus similar to, but less pronounced than, the bulges in *C. embryum*.

Relative body depth at the pectoral fin base increases during larval development from 20.7% in preflexion larvae to 28.5% SL in transforming larvae and juveniles.

Larval *C. globiceps* have a notably blunt,

rounded head and snout with relative head length increasing from 17.0% in preflexion larvae to about 31% SL in transforming juveniles.

FIN DEVELOPMENT.—The smallest larva beginning to undergo flexion of the notochord is 6.2 mm long. Notochord flexion is complete in larvae between 7.5 and 8.0 mm long. Although caudal rays are present in late-flexion stage larvae (7.0–7.5 mm NL), the adult complement of 6 + 6 principal caudal rays is not countable until the completion of flexion at 7.4 mm.

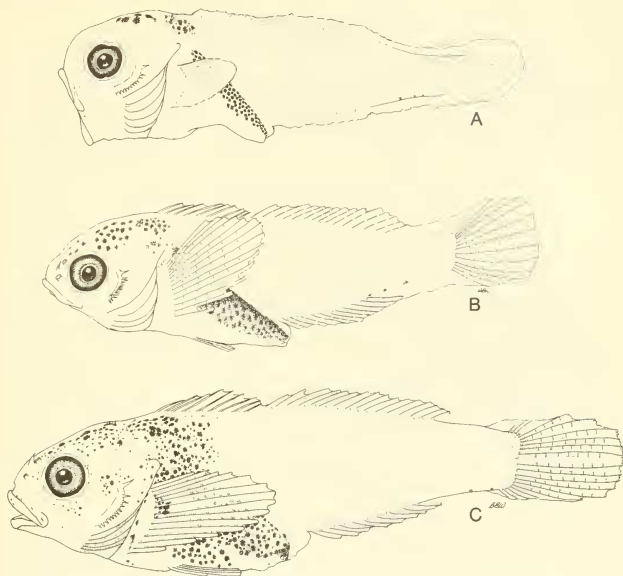


FIGURE 27. Larvae of *Clinocottus globiceps*: A) 8.5 mm SL, B) 12.5 mm SL, C) 12.9 mm SL (B from Richardson and Washington 1980).

Dorsal and anal fin bases are just beginning to form at completion of notochord flexion. The full complement of dorsal (13–17) and anal (11–12) fin rays is complete at ~9.5 mm. The dorsal spines (VIII–X) are completely formed at ~10 mm. Development of the pectoral fin corresponds to that of the dorsal and anal fins. Pectoral fin rays are visible on a 7.5 mm larva. The adult complement of rays (13–15) is fully formed by ~9–9.5 mm. Pelvic fin buds are first visible in larvae between 6.5 and 7 mm long. The adult complement (I,3) is present between 9.5 and 10 mm.

SPINATION.—Preopercular spines first appear as seven to nine small bumps along the posterior

margin of the preopercle in larvae 5.5–6 mm. Larvae undergoing notochord flexion have 9–14 small, evenly spaced spines along the preopercular margin. During postflexion, spines increase in number from 16 to 22, and the dorsalmost spine becomes separated from the rest of the preopercular spines by a short gap. Simultaneously, this dorsalmost spine becomes longer and stouter than the other preopercular spines. In the largest planktonic larvae (12.5 mm SL) this dorsalmost spine is about 2.5 times as long as the other spines. The lower preopercular spines decrease in size and number during transformation. The uppermost spine continues to become longer and stouter in benthic juveniles and is over four times

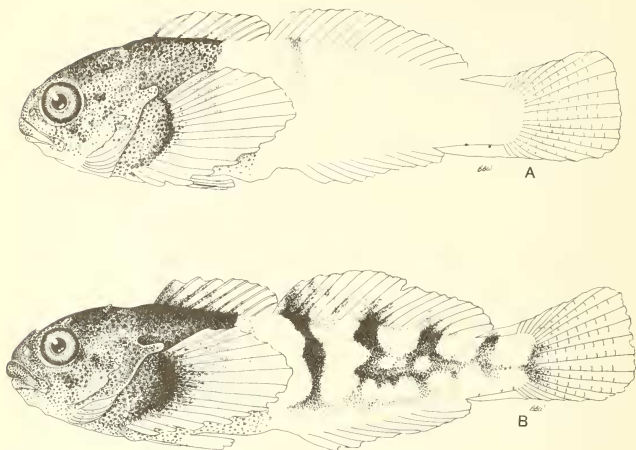


FIGURE 28. Juveniles of *Clinocottus globiceps*: A) 13.7 mm SL, B) 14.6 mm SL.

as long as the lower spines in a 14.5 mm specimen. The other preopercular spines are reduced to small bumps or serrations along the lower preopercular margin. In a 17-mm juvenile all remnants of the lower spines have disappeared and only the large dorsal spine persists.

Clusters of spines develop on the head in the parietal region of *C. globiceps* larvae. One tiny spine is visible on each side of the head in larvae 6–7 mm and two spines are present on each side of the head in larvae 7–8 mm. By ~9–10 mm, five to six spines are present on each side of the head, arranged in a parallel pair of rows with two to three spines in the anterior row and three spines in the posterior row. These spines persist in the largest planktonic specimens examined (12.9 mm). In newly settled benthic juveniles, however, these spines appear reduced and are present only as bony protuberances situated at the posterior margin of the parietals. Each protuberance has a hollow canal running through it which eventually forms the incipient cranial lateral line system in the parietal region of the head.

Similar spine clusters also form in the supra-leithral-posttemporal region. One or two small spines are first visible in larvae ~9 mm long. Five or six spines, arranged in two rows of three spines each, are present in both of the 12-mm specimens. These spines eventually become associated with the lateral line system in benthic juveniles.

Clinocottus analis

(Figure 29; Table 6)

LITERATURE.—Eigenmann (1892) and Budd (1940) briefly described and illustrated 4-mm specimens of *C. analis*.

IDENTIFICATION.—Juveniles and adults were identified by the following combination of characters: an advanced anus, cirri, head shape, and pigmentation. Pigmentation, preopercular spination, and body shape linked postflexion larvae of *C. analis* with juveniles and adults.

DISTINGUISHING FEATURES.—Late postflexion and transforming specimens of *C. analis* were identified in collections from southern Califor-

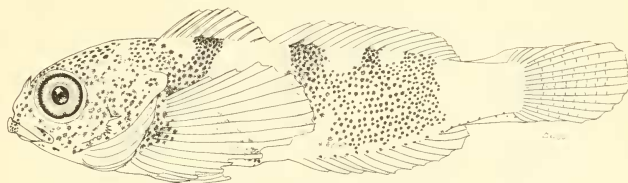


FIGURE 29. Young of *Clinocottus analis*: 10.5 mm SL.

nia. Apart from the two descriptions of newly hatched larvae, intermediate larval stages of *C. analis* are unknown. A brief diagnosis of postflexion larval *C. analis* is presented in the hope that this information may facilitate the identification of a complete developmental series of *C. analis*.

Eleven postflexion larval *C. analis* (9.9–11.4 mm SL) were examined for developmental morphology, pigmentation, and spination. *Clinocottus analis* postflexion larvae may be distinguished from all other larvae belonging to the *Arteidius*, *Clinocottus*, *Oligocottus* groups by the intense band of melanistic pigmentation on the lateral body surface between the bases of the second dorsal and anal fins. Intense melanophores are also present on the dorsolateral surface of the head, the snout, the tips of the lips, and on the operculum. A patch of melanophores is present on the pectoral fin base and in a band on the dorsum beneath the spinous dorsal fin. Sixteen to 22 small, round melanophores are situated on the ventral midline posterior to the anus.

Postflexion larval *C. analis* have blunt, rounded snouts and relatively large heads. Snout length and head length are 28% HL and 30% SL, respectively, longer than in other *Clinocottus* larvae. In addition, *C. analis* larvae have moderately long, bulging guts. Snout to anus length averages 49% SL in postflexion larvae. Body depth at the pectoral fin base is 28% SL, while body depth at the anus is 26% SL.

Six to 11 spines are present on the posterior margin of the preopercle. The dorsalmost spine is longer and stouter than the other spines. In the smallest specimens (9.9–11.0 mm) the spines are situated in two groups of three to five spines. The ventralmost spines begin to regress in larvae > 11

mm long; these spines decrease in size and number and gradually become covered by skin. Two small spines are also present in the parietal region of the head in the 9.9 mm specimen. These spines decrease in size and remain only as bony bumps by ~11 mm.

Arteidius creaseri

(Figures 30, 31; Table 7)

LITERATURE.—Larval *Arteidius creaseri* have not been previously described.

IDENTIFICATION.—Juveniles and adults were identified by the following combination of characters: low dorsal fin ray (12–14) and anal fin ray (9–10) counts, low vertebral counts (30–31), scales extending onto head under the orbit and on the snout, and the presence of a preorbital cirrus. The developmental series was linked together primarily by preopercular and parietal spination, pigmentation, body shape, and meristics. Postflexion and transforming larvae were linked to juveniles by the cirri pattern, pigmentation, body shape, and meristics.

DISTINGUISHING FEATURES.—Preflexion larvae of *A. creaseri* are characterized by a pointed snout, large head, and relatively deep body. Distinguishing pigmentation includes intense, large, round melanophores covering the dorsolateral surface of the gut, 1–3 large melanophores at the anteroventral margin of the gut, and a series of 7–11 large, evenly spaced melanophores along the ventral midline posterior to the anus. A large, distinctive, blotch-like melanophore is located on the ventral finfold near the tail tip, and another smaller melanophore occurs just beneath the tail tip.

Larvae of *A. creaseri* > 7 mm are further distinguished by the presence of four large, evenly

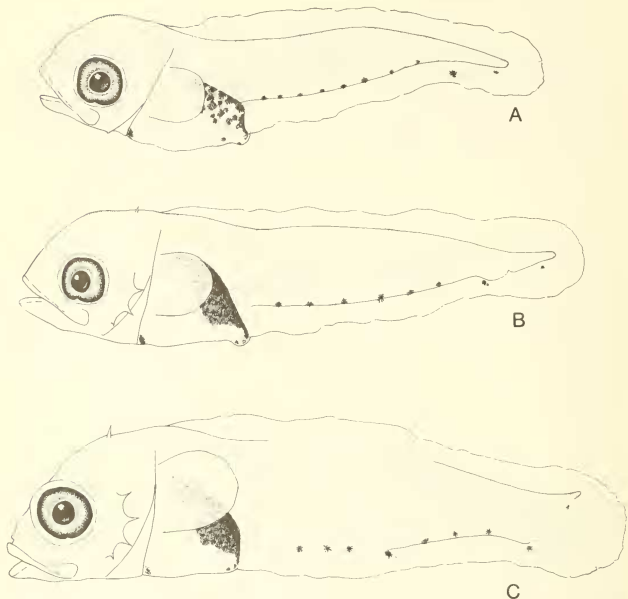


FIGURE 30. Larvae of *Artedius creaseri*: A) 5.0 mm NL, B) 6.6 mm NL, C) 7.9 mm SL.

spaced preopercular spines and a prominent parietal and nuchal spine. Late postflexion larvae may be recognized by their pointed snout and long jaw, large head, and the characteristic ventral midline pigmentation. In addition, meristics, especially the low dorsal fin, anal fin, and vertebral counts are diagnostic of this species. Small juveniles possess a long, slender nasal cirrus, a broad, ribbonlike postorbital cirrus with a fringed tip, and two pairs of frontoparietal cirri.

PIGMENTATION.—Small preflexion larvae of *A. creaseri* are relatively lightly pigmented. They possess no melanistic pigmentation on either the head or the nape. Pigmentation over the dorsolateral surface of the gut is heavy and intense.

Melanophores are large, round, and closely packed together. One or 2 melanophores are present on the ventral surface of the gut lying just posterior to the cleithrum. Posterior to the anus, the sole pigmentation consists of a series of 7–11 large, rounded melanophores evenly spaced along the ventral midline, positioned approximately 1 to every three myomeres. This series originates under the third or fourth post-anal myomere and extends posteriorly toward the tail tip. The posteriormost 1 or 2 melanophores in this series lie on the ventral finfold and are notable: large and blotchlike.

Pigmentation increases markedly during larval development. Two melanophores form over the

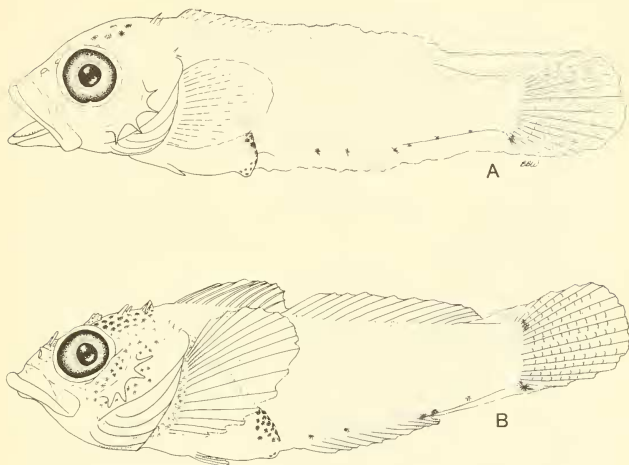


FIGURE 31. Larvae of *Artedius creaseri*: A) 9.1 mm SL, B) 13.0 mm SL.

midbrain in larvae >5.7 mm. During flexion, melanophores increase in number and extend anteriorly onto the forebrain. By ~ 8.0 mm, the dorsal surface of the head is entirely pigmented. Pigmentation extends dorsally along the anterior wall of the gut so that 3 or 4 large melanophores lie just posterior to the cleithrum. Several melanophores form at the posterior margin of the gut in larvae >6 mm, frequently forming a ring around the anus. The number of postanal ventral midline melanophores ranges from 6 to 12, and the 4th or 5th melanophore in the series increases markedly in size and extends below the body wall onto the ventral finfold. The posteriormost 2 melanophores in the series move up onto the base of the caudal finfold. One is positioned just posterior to the lower hypural plate and the other lies just below the tip of the notochord at the dorsal base of the upper hypural plate.

Transforming larvae (>10 mm) have melanophores extending ventrally along the preopercle and opercle and two to four melanophores

on the lower jaw. Pigment is also added on the pectoral fin.

MORPHOLOGY.—The smallest larval *A. creaseri* examined is 3.5 mm NL and recently hatched. Flexion of the notochord occurs between 5.7 and 7.9 mm NL. The largest planktonic specimen is 13 mm and beginning to develop juvenile pigmentation. The smallest benthic juvenile is 13.5 mm and still undergoing transformation. Thirty-two specimens ranging from 3.5 to 13.6 mm were measured for developmental morphology.

Artedius creaseri larvae are relatively deep-bodied with distinctively large heads and pointed snouts. Body depth at the pectoral fin base averages 26% in preflexion larvae and increases to 29% SL in postflexion larvae. Relative head length averages about 25% in preflexion and flexion larvae and increases to 33% SL in postflexion larvae. Snout length remains 30% HL during larval development.

FIN DEVELOPMENT.—Initiation of a thickening in the hypural region of the developing caudal

TABLE 7. BODY PROPORTIONS OF LARVAE AND JUVENILES OF *ARTEDIUS CREASERI* AND *A. MEANYI*. Values are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses.

Item	<i>Arteidius creaseri</i>	<i>Arteidius meanyi</i>
Head length/SL:		
Preflexion	24.4 ± 1.25 (22.9–26.5)	18.6 ± 1.77 (17.9–21.3)
Flexion	26.0 ± 2.46 (22.8–28.8)	22.7 ± 3.53 (19.4–38.0)
Postflexion	32.6 ± 3.80 (26.5–38.5)	32.1 ± 4.68 (25.4–38.0)
Juvenile	40.3 ± 2.97 (38.2–42.4)	–
Snout length/HL:		
Preflexion	29.7 ± 2.74 (25.0–33.0)	27.5 ± 7.50 (15.1–31.0)
Flexion	31.9 ± 3.58 (26.7–36.9)	29.5 ± 5.01 (22.3–35.4)
Postflexion	30.4 ± 2.95 (25.1–35.5)	29.4 ± 4.34 (23.1–37.3)
Juvenile	23.2 ± 1.20 (22.4–24.1)	–
Eye diameter/HL:		
Preflexion	42.0 ± 4.42 (34.7–47.3)	44.0 ± 3.39 (35.0–47.7)
Flexion	37.4 ± 3.11 (32.5–43.1)	36.6 ± 4.93 (30.4–43.1)
Postflexion	33.2 ± 4.01 (27.5–38.6)	29.0 ± 3.31 (23.2–35.3)
Juvenile	30.4 ± 1.20 (29.6–31.3)	–
Snout to anus length/SL:		
Preflexion	44.6 ± 3.01 (41.5–50.0)	33.0 ± 2.86 (27.2–35.4)
Flexion	43.5 ± 3.83 (39.7–50.0)	39.6 ± 2.97 (36.1–44.3)
Postflexion	51.5 ± 3.66 (44.6–55.8)	48.3 ± 4.43 (38.0–55.2)
Juvenile	54.4 ± 1.77 (53.2–55.7)	–
Snout to pelvic fin origin/SL:		
Preflexion	–	–
Flexion	–	23.0*
Postflexion	29.5 ± 2.17 (27.0–33.1)	29.1 ± 3.16 (21.9–33.6)
Juvenile	32.0 ± 2.12 (30.5–33.5)	–
Pelvic fin origin to anus/SL:		
Preflexion	–	–
Flexion	–	20.1*
Postflexion	24.6 ± 4.96 (17.5–33.9)	19.4 ± 1.60 (15.7–22.1)
Juvenile	22.4 ± 0.35 (22.2–22.7)	–
Body depth at pectoral fin base/SL:		
Preflexion	26.0 ± 2.54 (23.4–29.7)	18.0 ± 1.64 (16.2–20.0)
Flexion	26.0 ± 1.78 (22.7–28.1)	19.9 ± 1.25 (17.7–22.2)
Postflexion	28.8 ± 2.67 (25.3–33.8)	24.6 ± 3.65 (17.2–30.1)
Juvenile	24.8 ± 1.98 (23.4–26.2)	–
Body depth at anus/SL:		
Preflexion	21.8 ± 2.35 (19.4–26.0)	15.2 ± 3.11 (11.9–19.1)
Flexion	24.0 ± 3.08 (19.3–28.1)	18.9 ± 1.55 (15.8–21.3)
Postflexion	28.2 ± 3.07 (25.4–36.2)	24.6 ± 2.73 (19.3–28.4)
Juvenile	21.2 ± 2.19 (19.6–22.7)	–
Pectoral fin length/SL:		
Preflexion	–	8.4 ± 1.35 (6.4–9.1)
Flexion	12.2 ± 1.97 (9.5–15.1)	9.2 ± 1.77 (6.5–12.1)
Postflexion	23.7 ± 6.11 (14.5–35.2)	19.0 ± 6.21 (10.1–28.3)
Juvenile	30.1 ± 1.34 (29.1–31.0)	–

– = Not present at this stage.

* = Only one specimen available at this stage.

fin is first evident at 5.7 mm, coincident with the onset of notochord flexion. Caudal rays are present at 6.4 mm, but the adult complement of 6 +

6 principal caudal rays is not present until larvae reach ~8.0 mm.

Bases of the second dorsal (12–14) and anal

(9–11) fins are countable in larvae ~7–8 mm long, and fin rays are formed between 9 and 10 mm. The adult complement of dorsal fin spines (IX–X) is first countable at 9.7 mm. Pectoral fin rays begin forming at ~7–8 mm, and the adult complement is present at 8.6 mm. Pelvic buds begin to form at >8 mm; however, the adult complement of rays is not present until larvae are >11 mm.

SPINATION.—*Artedius creaseri* larvae develop prominent head spines. In contrast to *Artedius*, *Clinocottus*, and *Oligocottus* larvae which have multiple preopercular spines, *A. creaseri* larvae develop four equal-sized preopercular spines. Two spines develop first on the posterior margin of the preopercle at >5.7 mm. At a state of growth between ~6.4 and 7 mm, two additional spines develop, one dorsal and one ventral to the original two spines. The middle two spines remain slightly longer than the outer two throughout larval development. These spines persist through transformation and are present in juveniles. In larvae >10 mm, small basal spines or projections form on the base of each of the four main preopercular spines. With development, four bony ridges form on the inner shelf of the preopercle parallel to each basal spine. These ridges grow toward the basal spines and gradually fuse with them forming bony arches over the incipient lateral line canal of the preopercle. Prominent spines also form in the parietal region of the head. A single parietal spine is first visible at 5.7 mm. By >9 mm, a second smaller parietal spine forms just posterior to the first. These spines are quite large and distinctive, and they are present in the largest planktonic larvae (>13 mm long).

When larvae reach ~8 mm, a spine forms in the supracleithral-posttemporal region. The supracleithral spine points dorsolaterally. A second supracleithral spine forms just ventral to the first and points dorsally. Larvae >9.5 mm form one posttemporal spine. These spines persist in the largest planktonic larvae (13.6 mm) but regress in young juveniles becoming incorporated into the developing lateral line canal system.

Artedius meanyi

(Figures 32, 33; Table 7)

LITERATURE.—Blackburn (1973) described a 4.3-mm larva resembling *A. meanyi*, which he called Cottid 3. Richardson (1977) and Richardson and Pearcy (1977) listed three larvae as *Ice-*

linus sp. 1. Richardson and Washington (1980) illustrated and described specimens 3.3, 8.6, 10.9, 12.5, 13.5, 15.2, 16.5, and 16.6 mm long as *Icelinus* spp.

IDENTIFICATION.—Larval *A. meanyi* were misidentified as *Icelinus* spp. by Richardson and Washington (1980) on the basis of meristics and the pelvic fin ray count of 1,2, which is characteristic of *Icelinus*. Meristics also match those of *A. meanyi*, which possess 1,3 (rarely 1,2) pelvic fin rays (Rosenblatt and Wilkie 1963; Lea 1974). Recently, Howe and Richardson (1978) reexamined Lea's specimens of *A. meanyi* and reported that "... only one small specimen appeared to have two rays—all others had three rays." Lea's specimens were reexamined in this study. Cleared and stained specimens clearly have 1,2 pelvic fin rays. The outermost ray is greatly thickened and branched at the tip in all specimens examined. All of the misidentified "*Icelinus*" larvae possess this distinctive, thickened outer ray.

In addition, during the present study, large transforming specimens of *A. meanyi* were obtained that possess scales on the dorsal surface of the head, the opercle, and in four or five rows on either side of the dorsal fins. Specimens also possessed preorbital cirri and distinctive postocular cirri with three tentacles arising from a single base. The combination of these morphological and meristic characters conclusively identifies these transforming larvae and juveniles as *A. meanyi*. The developmental series was linked together primarily on the basis of pigmentation and body shape.

DISTINGUISHING FEATURES.—Small preflexion larval *A. meanyi* are distinguished by their short, compact guts (snout to anus length averages 33% SL) and pointed snouts. Characteristic pigmentation includes a low number of ventral midline melanophores posterior to the anus (<13), several large melanophores situated anteriorly on the visceral mass at the base of the cleithrum, and two distinctive blotches of pigment on both the dorsal and anal finfolds.

Notochord flexion begins at a relatively large size, ~6.2 mm in *A. meanyi* larvae, and is complete by ~9.4 mm. Four large, evenly spaced spines form along the margin of the preopercle in postflexion larvae >9 mm. Two parietal spines develop at the posterior margin of each parietal in larvae >11 mm.

Postflexion and juvenile *A. meanyi* (13–18 mm

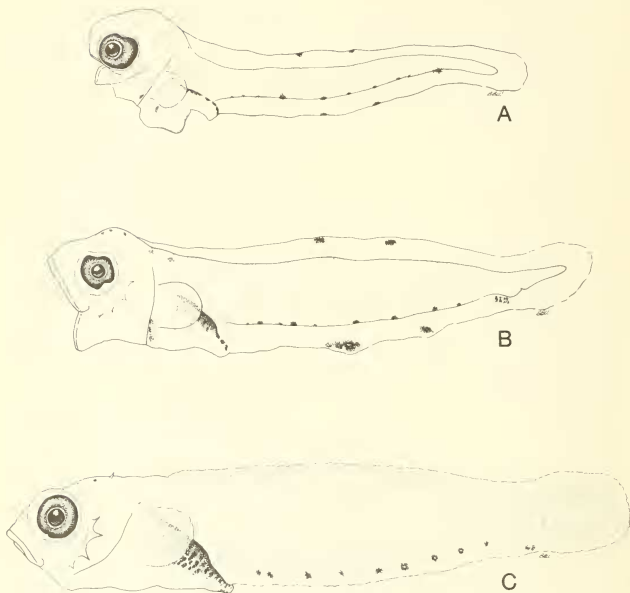


FIGURE 32. Larvae of *Artedius meanyi*: A) 3.3 mm NL, B) 8.6 mm NL, C) 10.9 mm NL (from Richardson and Washington 1980).

long) are distinguished by a low number of blotchy ventral midline melanophores posterior to the anus, a relatively pointed snout and large head (33% SL), a pelvic fin ray count of I,2 with the outermost ray thickened as if two rays are fused together, and other meristics. In addition, juvenile *A. meanyi* possess a single, slender preorbital cirrus, an eyeball cirrus, and a distinctive postorbital cirrus having three tentacles that arise from a single base. The largest specimens (16–18 mm) possess rows of prickle-like scales on the parietal, cheek, and opercular regions of the head and on the dorsal surface of the body and caudal peduncle.

PIGMENTATION.—Small *A. meanyi* larvae are relatively lightly pigmented. Melanistic pigmentation is absent on the head of preflexion larvae. Two to 5 round, external melanophores are clustered on the nape. The dorsolateral surface of the gut is lightly pigmented. Two or 3 large dendritic melanophores are embedded in the anterior musculature of the body cavity just posterior to the cleithrum. Posterior to the anus, a series of 7–13 large, blotch-like melanophores is positioned along the ventral midline originating under the second to fourth postanal myomere and extending toward the tail tip. These melanophores vary in size with the 3rd or 4th and the

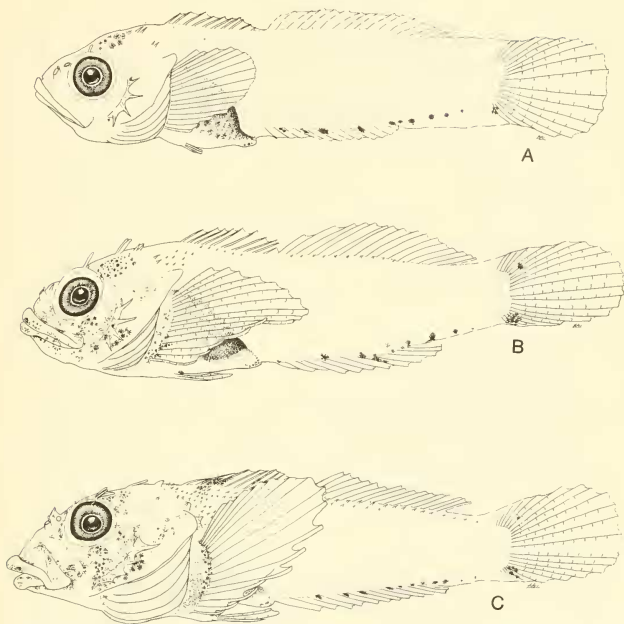


FIGURE 33. Young of *Artedius meanyi*: A) 13.8 mm SL, B) 15.2 mm SL, C) 16.5 mm SL (from Richardson and Washington 1980).

posteriormost melanophores of the series being markedly larger and frequently extending onto the ventral finfold. Two large distinct pigment blotches are present on both the dorsal and ventral finfolds in small larvae. One specimen out of 45 examined possessed three pigment spots on both the dorsal and anal finfolds.

Melanistic pigmentation increases during larval development. Several melanophores are added over the brain in larvae between 7.4 and 8 mm. Melanophores in the nape region become embedded in larvae > 6 mm as body musculature develops. Pigmentation increases slightly over

the lateral surfaces of the gut. With the onset of notochord flexion and development of the caudal fin, the posteriormost melanophore of the ventral midline series is characteristically positioned at the ventral margin of the forming caudal fin. A second, large melanophore is frequently added at the dorsal margin of the caudal fin base dorsal to the notochord tip. The blotches of pigment on the dorsal and ventral finfolds disappear in larvae > 9 mm as fin rays begin to form.

During transformation, between 13 and 19 mm, head pigmentation increases markedly. Melanophores extend anteriorly over the interor-

bitar region and onto the snout. Several melanophores are added just ventral to the orbit, between the eye and preopercle, and along the dorsal margin to the opercle. With development, melanophores are also added along the pectoral fin base, in a band across the dorsum, and on the dorsal fin around the first four dorsal spines. Melanophores are also added to the upper and lower lips, across the cheek, along the ventral margin of the opercle, and on the dorsal surface of the head.

MORPHOLOGY.—The smallest larval *A. meanyi* collected from plankton samples are ~3 mm NL long and appear recently hatched. Larvae undergo notochord flexion between 6.2 and 9.4 mm NL. Specimens as large as 18–19 mm were collected in plankton and neuston tows. Planktonic larvae >15 mm are beginning to undergo transformation indicated by the development of juvenile pigmentation and the formation of scales on the head and dorsum. The smallest benthic juveniles examined were 15–16 mm long and were fully transformed. Thirty specimens, ranging in size from 3.3 to 17.9 mm, were examined for morphometrics.

Small larval *A. meanyi* are relatively slender with a characteristic body shape. Body depth is constricted just posterior to the anus; the body bulges slightly in the midtail region and narrows again near the tail tip or caudal peduncle. This distinctive body shape remains apparent throughout larval development. The gut of *A. meanyi* is short and tightly coiled. Snout to anus length averages 33% SL in preflexion larvae increasing markedly to 48% in postflexion larvae. Prior to flexion of the notochord, body depth averages 18% at the pectoral fin base and 15% SL at the anus and increases to 25% SL at both the pectoral fin base and the anus in postflexion larvae and juveniles.

Artedius meanyi larvae have small heads with a distinctively pointed snout. Head length averages 19% in preflexion larvae, then increases dramatically to 33% SL in late postflexion larvae and juveniles. Snout length remains relatively constant throughout larval development, ranging from 28 to 30% HL.

FIN DEVELOPMENT.—The fins develop relatively late in *A. meanyi*. Initiation of notochord flexion begins at ~6.2 mm NL. Although caudal rays are first visible in larvae >7 mm long, principal caudal ray number (6 + 6) is not complete until after notochord flexion at ~11 mm. Dorsal

and anal soft rays begin to form in larvae 9.5–10 mm long. The full complement of fin rays is visible in larvae ~12 mm. Dorsal spines (IX–X) begin to form at ~11 mm and are all present by 12–13 mm. Pelvic fin buds form in larvae >9.5 mm; however, the adult complement of pelvic fin rays (1,2) is not complete until larvae reach ~12–13 mm.

SPINATION.—Preopercular spines form relatively late in the development of *A. meanyi* larvae. Two tiny spines are first visible along the central portion of the preopercle in larvae >6.2 mm with a third spine forming dorsal to these spines between 8 and 8.5 mm. By 9.4 mm, a fourth spine is added at the ventral margin of the preopercle. These four spines remain prominent and approximately equal-sized throughout larval development. In larvae >13 mm, small basal spines or projections form on the base of each of the four main preopercular spines. With development, four bony ridges form on the inner preopercular shelf parallel to each basal spine. These ridges grow toward the basal spines and gradually fuse with them forming bony arches over the incipient lateral line canal of the preopercle. During transformation, between 15 and 17 mm, the dorsalmost preopercular spine becomes longer and stouter than the other spines; however, all four preopercular spines remain clearly visible on the largest pelagic juveniles examined (~19 mm long).

Spines also develop in the parietal and supra-cleithral-posttemporal regions of the head. A single tiny spine first forms at the posterior margin of the parietal in larvae >7 mm long. This spine gradually becomes longer, and in larvae between 12 and 13 mm a second, smaller nuchal spine forms immediately posterior to it.

A small spine forms on the dorsal margin of the posttemporal bone between 9 and 10 mm. A second, similarly sized spine is added ventrally on the posttemporal in larvae ~11 mm. At about the same time, a third spine forms posterovertrally to the two posttemporal spines on the dorsal portion of the supra-cleithrum. These three spines increase in size during transformation and eventually become associated with the junction of the cephalic and lateral line systems.

ADDENDUM

Since this study was accepted for publication, a subsequent review of cottid relationships has been published (Washington et al. 1984). Wash-

ington et al. (1984) presented a hypothesis of phylogenetic relationships of cottoids and briefly summarized characters that supported eight proposed monophyletic groups of cottid genera. Much of this work was based on an unpublished manuscript (Washington and Richardson n.d.) in which a hypothesis of cottid relationships based on osteological characters of early life history stages was presented. Results of Washington et al. (1984) support the proposed monophyly of *Artedius* Group A, *Clinocottus*, and *Oligocottus* and the exclusion of *Artedius creaseri* and *A. meanyi* from this group. They listed five synapomorphic characters in addition to the multiple preopercular spines which support the monophyly of *Artedius* Group A, *Clinocottus*, and *Oligocottus*. These characters include anterior neural arches enlarged and elevated, arms of the anterior neural arches open in a broad u-shape until late in the juvenile period, a greatly expanded cleithrum base, posterior extensions or bony plates at the cleithrum base which enclose the pelvic bones, and loss of ventral postcleithrum and reduction or loss of dorsal postcleithrum.

Washington et al. (1984) also placed *Artedius creaseri* and *A. meanyi* in a proposed monophyletic group of genera including *Icelinus* and *Myoxocephalus* as well as 10 other cottid genera. This placement gives additional evidence for the exclusion of *Artedius creaseri* and *A. meanyi* from the genus *Artedius* (sensu Bolin 1944) and supports their close relationship to *Icelinus* and *Myoxocephalus*. Further results of Washington et al. (1984) provide additional characters that strengthen the hypothesis of monophyly of *Artedius* Group A, *Clinocottus*, and *Oligocottus*.

ACKNOWLEDGMENTS

I am indebted to many people for the loan of materials. Dr. Geoffrey Moser, National Marine Fisheries Service, La Jolla; Dr. Richard Rosenblatt, Scripps Institution of Oceanography, La Jolla; Dr. Robert Lavenberg, Los Angeles County Museum, Los Angeles; H. J. Walker, Ecological Marine Consultants, Solano Beach; Dr. William Eschmeyer, California Academy of Sciences, San Francisco; David Rice, Lawrence Livermore Laboratory, Livermore; Dr. Arthur Kendall, National Marine Fisheries Service, Seattle; Dr. Theodore Pietsch, University of Washington, Seattle; Dr. Norman Wilimovsky, University of British Columbia, Vancouver; and Dr. Jeffrey Marliave, Vancouver Public Aquarium, Van-

couver; all were helpful in making materials in their collections available to me.

Special thanks are due Dr. Robert Morris for generously allowing me access to an unpublished manuscript on laboratory-reared *Oligocottus snyderi* larvae. I would also like to thank Kevin Howe, Joanne Laroche, Wayne Laroche, James Long, Bruce Mundy, Dorinda Ostermann, and Waldo Wakefield for volunteering their help in tidepool sampling. I gratefully acknowledge Dr. William Percy for his encouragement and for providing laboratory space. Special thanks are due to Kevin Howe for stimulating conversations about cottid relationships, for reviewing parts of this manuscript, and for first teaching me about sculpins. I wish to thank Dr. Carl Bond, Wayne Laroche, and Dr. Sally Richardson for helpful discussions about cottids and for reviewing initial drafts of this manuscript.

I gratefully acknowledge Margaret Snider and Lucia O'Toole for carefully typing drafts of this paper.

This study was funded in part by Oregon State University Sea Grant College Program supported by NOAA Office of Sea Grant, Department of Commerce and by a Grant-in-Aid of Research from Sigma Xi, The Scientific Research Society of North America.

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- Note: Since this paper went to press, a phylogenetic study of the Cottoidea has been published that addresses relationships of 42 cottid genera including *Artedius*, *Clinocottus*, and *Oligocottus* (Yabe 1985). A discussion of Yabe's work will be included in a forthcoming paper (Washington and Richardson n.d.).
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